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MOSCOW STATE UNIVERSITY

ACTA

XVIII

CONGRESSUS INTERNATIONALIS ORNITHOLOGICI

Moscow, August 16–24, 1982

VOLUME I

Editors: V.D. ILYICHEV and V.M. GAVRILOV



MOSCOW "NAUKA"
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XVIII CONGRESSUS
INTERNATIONALIS ORNITHOLOGICUS

Moscow, August 16—25, 1982

ACTA
Volume I

This volume contains full text of plenary lectures, papers and any abstracts of forenoon symposia:

Paleontology and evolution of birds

Sensory organs and communication in birds

New problems of orientation

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INTERNATIONAL ORNITHOLOGICAL CONGRESSES 1884-1982

| | Place | Year | President | Secretary-General |
|-------|------------|------|---|--------------------------------------|
| I | Vienna | 1884 | Dr. G.F.R.Radde | Dr. Gustav von Hayek |
| II | Budapest | 1891 | Prof. Victor Fatio und Otto Herman | - |
| III | Paris | 1900 | Dr. Emile Oustalet | Jean de Claybrooke |
| IV | London | 1905 | R.Bowdler Sharpe | Dr. E.J.O.Hartert J.Lewis Bonhote |
| V | Berlin | 1910 | Prof. Dr.Anton Reichenow | Herman Schalow |
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| X | Uppsala | 1950 | Dr. Alexander Wetmore | Prof. Dr. Sven Hörstadius |
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| XII | Helsinki | 1958 | Prof. J.Berlioz | Dr. Lars von Haartman |
| XIII | Ithaca | 1962 | Dr. Ernst Mayr | Dr. Charles G.Sibley |
| XIV | Oxford | 1966 | Dr. David Lack | Prof. Dr. N.Tinbergen |
| XV | Den Haag | 1970 | Prof. Dr.Nikolaas Tinber- gen, 1966-1969 Prof. Dr.Finn Salomonsen, 1969-1970 | Prof. Dr. Karel H.Voous |
| XVI | Canberra | 1974 | Prof. Dr.Jean Dorst | Dr. H.J.Frith |
| XVII | Berlin | 1978 | Prof. Dr. D.S.Farner | Rolf Nöhring |
| XVIII | Moscow | 1982 | Prof.Dr.Lars von Haartman | Prof. Dr. V.Ilyichev |

ACTA OF PRECEDING INTERNATIONAL ORNITHOLOGICAL CONGRESSES

- I. Sitzungs-Protokolle des ersten Internationalen Ornithologen-Congresses, der vom 7. bis 11. April 1884 in Wien abgehalten wurde. Wien, Verlag des Ornithologischen Vereines in Wien, 1884, vi+ 90 p.
Mitteilungen des Ornithologischen Vereins Wien, Band xiii-x, 1884-86.
- II. Bericht... Zweiter Internationaler Ornithologischer Congress, Budapest, 1892. (Blasius) n.p.; 1891, 58 p.
- III. III^e Congrès Ornithologique international, Paris/26-30 juin 1900. Compte rendu des séances publié par E.Oustalet... et J.de Claybrooke... Masson et Cie, Paris. xii+503 p. 1901 [Ornis, vol. 11]
- IV. Proceedings of the Fourth International Ornithological Congress, London/June 1905. Edited by R.B.Sharpe, E.J.O.Hartert, and J.L.Bonhote. Dulau & Co., London. 696 p. 1907. [Ornis, vol. 14]
- V. Verhandlungen des V.Internationaler Ornithologen-Kongresses, Berlin 30. Mai bis 4. Juni 1910. Herausgegeben von Herman Schalow... Deutsche Ornithologische Gesellschaft, Berlin. x+1186 p. 1911.
- VI. Verhandlungen des VI.Internationalen Ornithologen-Kongresses in Kopenhagen, 1926. Herausgegeben von Dr. F.Steinbacher. Berlin. vi+ 641 p. 1929.
- VII. Proceedings of the VIIth International Ornithological Congress at Amsterdam. Amsterdam. vii+527 p. 1931.
- VIII. Proceedings of the Eighth International Ornithological Congress, Oxford/July 1934. Edited by F.C.R.Jourdain. Oxford University Press, Oxford. x+761 p. 1938.
- IX. IX^e Congrès Ornithologique International, Rouen /9 Au-13 Mai 1938. Compte Rendu publié par Jean Delacour... Rouen. 543 p. 1938.
- X. Proceedings of the Xth International Ornithological Congress, Uppsala/ June 1950. Edited by Sven Hörstadius. Almqvist & Wiksells, Uppsala. 662 p. 1951.
- XI. Acta XI Congressus Internationalis Ornithologici, Basel/29.V -5.VI 1954. Herausgegeben von Adolf Portmann und Ernst Sutter. Birkhäuser Verlag, Basel und Stuttgart. 680 p. 1955.
- XII. Proceedings/XII International Ornithological Congress/Helsinki. 5. - 12.VI 1958. Edited by G.Bergman, K.O.Donner, L.v.Haartman. Tilgmannin Kirjapaino, Helsinki. 2 vol. 820 p. 1960.
- XIII. Proceedings XIII International Ornithological Congress, Ithaca/17-24 June 1962, Editor: Charles G.Sibley. Published by The Ornithologist's Union, Baton Rouge, Louisiana. 2 vol. xvi+1246 p. 1963.
- XIV. Proceedings of the XIV International Ornithological Congress, Oxford/ 24-30 July 1966. Edited by D.W.Snow. Blackwell Scientific Publications, Oxford and Edinburgh. xxiv+405 p. 1967.
- XV. Proceedings of the XVth International Ornithological Congress, The Hague/ 30 August-5 September 1970. Edited by K.H.Voous. E.J.Brill, Leiden. viii+745 p. 1972.
- XVI. Proceedings of the 16th International Ornithological Congress, Canberra/ 12-17 August 1974. Edited by H.J.Frith and J.H.Calaby. Australian Academy of Science, Canberra. xviii+765 p. 1976.
- XVII. Acta XVII Congressus Internationalis Ornithologici, Berlin/5-11 June 1978. Herausgegeben von Rolf Nöhring. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin. Bds.2, 1464 S, 1980.

PREFACE

The XVIII International Ornithological Congress was the first one held in Slavolanguag country, so the organizers faced some difficulties during its preparations of Proceedings.

Following the tradition of the previous Congresses the Proceedings were named in Latin. Materials were presented in two volumes whose general composition is almost the same as in the Proceedings of the previous Congress. The numerical order of symposia is the same as in the pregress publication.

It was decided to publish only plenary lectures and forenoon symposia reports. The authors' original texts were printed with some corrections because only two conveners - V.R.Donik and D.S.Farner - have verified and edited the papers of their symposia before the publication.

At first we decided to publish the afternoon symposia papers in the form of conveners' reports. Later we had to abandon this plan because of great variation of the reports. We came to a compromise decision - to publish the most complete information (i.e. author's summary was preferable since it was more informative than the convener's report).

The abstracts of posters were published almost in the form of their pregress publications, and only few of them were rejected by their authors.

The Publication Commission received very few reports on the round table discussions, and all of them had been printed without any alterations.

We must apologize for some delay in issueing of this book because of the organizational problems, and also for possible mistakes in the text.

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INTERNATIONAL CO-OPERATION AND INTEGRATION WITH OTHER SCIENCES -
THE MAIN TREND OF ORNITHOLOGY DEVELOPMENT

V.D.Ilyichev

Each congress is a signal event in the development of ornithology. It marks the Centenary of International Ornithological Congresses, making us take stock of our progress in the past and meditate upon our prospects for the future.

During these years ornithology has attained much and advanced considerably, both as a science and a field of human practical activity. Its role in human life and in the economic domain, as well as its social and scientific prestige, have been greatly enhanced.

All of us welcomed the signing by many nations of intergovernmental conventions, relating to the study and conservation of birds and their habitats. The Ramsar Convention on Wetland of International Importance, Especially as Waterfowl Habitat, the Convention on International Trade in Endangered Species of World Fauna and Flora, and a number of others have been elaborated and signed during the last few decades.

Yet the concern of governmental bodies for birds did not develop by itself, being generated as a result of laborious efforts of numerous professionals and amateurs from all over the world. International co-operation of ornithologists has established a scientific and practical basis for these important arrangements to be implemented.

This Congress is supposed to draw a line under rather a long period in the development of ornithology, being one of the most ancient sciences. A hundred years is a considerable space in the history of science in such dynamic and eventful time as ours. New disciplines and fields of research have come into existence during this period, new basic facts have been established, and the most important fundamental and practical problems solved.

But the period in question must also be considered in the light of foregoing events since it represents a sequel to our predecessors' contribution and a base for our descendants to built on. It is important for us to identify such linkages and establish the principal trends in the development of ornithology.

In this context an active and ever-extending international co-operation, as well as integration of ornithology with other scientific and practical spheres of human activity, should be treated as a most significant trend that takes the lead in guiding the advance in this science.

Of course, this tendency implies first and foremost practical arrangements in the field of ornithology and bird conservation which are already successfully implemented through joint efforts of different nations. Considerable progress has been achieved along these lines.

At the same time the above tendency reflects ornithologists striving for new goals, unattainable in the past but made easier to achieve due to this very tendency.

These developments gave ornithologists an opportunity of operating with the two most important ecological parameters characterizing the existence of birds on the planet, viz. their numbers and ranges. Methods of quantitative analysis have thus been introduced into ornithological studies.

The tendency in question was even more essential for the expansion of ornithology into other scientific and practical realms, being so vital for human activity. They include ecomonitoring, environmental pollution and management of the biosphere to the benefit of mankind.

All this is certain to estrange modern ornithology from its traditional autonomous status of studying birds for the sake of birds. This major course of ornithology development is sure to be always retained. But is it all that is needed today?

Birds acquire an ever-increasing significance in human life and can no longer be disregarded as a source of serious danger to aircraft, grain farming and horticulture, as well as carriers of air-borne viruses giving rise to grave diseases in man and domestic animals, etc.

Birds act as agents of biological control of pests, restricting population outbreaks of the locust and other insects, and thus supplementing or sometimes substituting for chemical substances. They are important as a source of protein food components for man.

Birds are suppliers of the genetic fund indispensable for artificial selection and securing life on the planet in all its varieties and manifestations.

Ornithology has always been a supplier of biological models to be used in basic research. I wish to remind you of the ornithologists' contribution made to the general theory of evolution. Darwin, too, made the most of ornithological data that he had obtained and analysed as skilfully as any authority in the field. Huxley, Kleinschmidt, Rensch and other experts in the theory of evolution were professional ornithologists. The same is true of Professor Meyer a prominent evolutionist.

A most valuable contribution was made by ornithologists to such a basic biological discipline as ethology. We are fully aware of the role played by birds in the development of ethology and the research of Lorenz, Tinbergen, and other ethologists.

The model-supplying function of ornithology has been increasingly gaining in importance, its methodology being adapted to solving global ecological problems of optimal relationship between man and wildlife and between man and the environment.

Those attending the first Ornithological Congress could hardly realize that they were laying the keystone of international co-operation identifying the lines of development of this science for many years ahead.

The first Congress became a sort of preference point to mark off the progress achieved by next generations. Those were just initial steps, taken - and

this is notable - by none other than ornithology and giving other sciences a lead.

Birds as a biological entity gave an impetus to international collaboration. Inhabiting the air and moving freely over immense spaces of the planet, birds know no frontiers between nations or continents thus prompting ornithologists to co-operate.

Ornithologists had accumulated experience of coordination, and co-operation at a national level by the time of their first Congress. Another course of collaboration with other biological disciplines emerged, yielding its first results during expeditions of Pallas in the second half of the 18th century, sponsored by the Russian Academy of Sciences and covering vast areas of Eastern Europe and Northern Asia.

First partners of ornithologists were botanists and zoogeographers, followed by taxonomists and evolutionists, and still later by physiologists, etc. In the middle of the 20th century physicists, chemists, and mathematicians joined the ornithological research that can not be conceived today without active participation of representatives of exact sciences.

It is precisely due to this collaboration that ornithology has turned out to be among "the founders" of such important branches of general biology as signalization and communication, behaviour control, orientation, etc. Ornithology replenished the stock of its methods with new techniques and experimental approaches. Today the ornithologist has aircraft and radar controls under his thumb, there are biotelemetric and sound analyzing facilities along with computers at his disposal as well as scanning microscopes, biochemical centrifuges, and chemical reagents on his table.

International Ornithological Congresses were instrumental in the making and development of this tendency.

The first Congress was held in Vienna in 1884 and presided over by Dr. Radde. Another sixteen Congresses have been convened since then, with the last one opening here in Moscow today.

The International Ornithological Committee coordinated the work of ornithologists in different countries in the intervals between Congresses. It has established close contacts with the International Union of Biological Sciences and was incorporated as an autonomous section into it. The activities within the Union promoted closer collaboration of ornithologists with representatives of related sciences.

Notable contribution to this process was made by Professor D. Farner, president of the 17th International Ornithological Congress, who was the first to suggest Moscow as the Venue of the 18th Congress. It is my privilege to express our deep appreciation to Professor D. Farner for his extensive efforts.

Each Congress promoted contacts and joint efforts between ornithologists dealing with specific branches of knowledge and particular science junctions, forming a basis for new avenues of co-operation.

Thus the International Council for Bird Preservation (ICBP) was founded in 1922 already (with no other permanent body for nature conservation in operation at that time). It was followed by the establishment of the International

Waterfowl Research Bureau (IWRB) in 1952 and of the International Bird Ringing Committee (IBRC) - in compliance with the Resolution of the 13th International Ornithological Congress in 1962.

The autonomous development of ornithology was accompanied by its intensive expansion into related spheres of human scientific and practical activity.

A tangible contribution is made by ornithologists to the work of the International Union for the Conservation of Nature and Natural Resources. This organization deals with practical aspects of nature conservation and its activity results in the elaboration of intergovernmental conventions.

International co-operation in the field of aircraft protection against birds has been gaining momentum during the last few decades. It is for a long time now that ornithologists have been effectively working within the International Civil Aviation Organization (ICAO). The 16th annual meeting of this body is to take place simultaneously with the Congress here in Moscow.

Concerted efforts of ornithologists at international level have brought them to participation in global UNESCO-sponsored programmes of environmental conservation - MAR and MAB.

This signifies transition of ornithology to a higher stage of international collaboration, i.e. from intra- to interdisciplinary co-ordination, thus reflecting the inner logic of the development of international collaboration as well as that of ornithology.

The activity of international bodies is supposed to have more than just practical implications. It is also of great scientific importance, as it helps to resolve - on the basis of co-operation - a number of problems using techniques otherwise unavailable. Co-operation means both new methods and advanced scientific methodology. Some results of migratory bird studies may be cited to illustrate the importance of international contacts for the development of ornithology and management of practical problems facing mankind.

Although bird passage studies are known to have been carried out at the dawn of ornithology, their crucial stage was reached at the turn of the 20th century, after the introduction of ringing techniques. Birdbanding constituted one of the initial forms of international co-operation, being its indispensable component.

Both further history of the birdbanding technique and its contribution to migration studies were therefore in close liaison with broadening collaboration at international level. By 1930, over one million of birds were banded annually, with nearly 30 birdringing centres engaged in this activity in 20 countries.

Birdringing centres of different nations were involved in this work, and they had to act together under the organizing and levelling influence of the method they were all employing. The demands for standardization in this field have become particularly pronounced in the post-war years, when bird-banding was undertaken on an ever-growing scale and co-operation was recognized officially as being exercised under the aegis of the International Bird Ringing Committee. Continental sections of the Committee sprang up, with UERING taking

the central position among them both traditionally and through historical circumstances. EURING has become a sort of international institution to develop scientific aspects of collaboration and furnish comprehensive methods and approaches thus enabling ornithologists from different countries to pool their efforts.

Pooling birdringing data into regional banks was essentially important. In the first place, it allowed to extend sections of migration routes disrupted by the frontiers between countries. It also added considerably to the total volume of data, owing to amalgamation of national banks, and favoured application of computer technology.

International co-operation in birdringing has yielded important scientific results.

A general outline of main migratory routes and principal ecogeographic features of bird migrations have been made out by the 1960s. Applying methodological principles of international collaboration, ornithologists proceeded to studying migrations of birds in different regions. Cooperative efforts of ornithologists from Poland, Bulgaria, Hungary, Czechoslovakia, and the Soviet Union have resulted in publication of the first three volumes of the joint monograph entitled "Migrations of Birds of Eastern Europe and Northern Asia". Other volumes are in preparation.

Studies undertaken in common by ornithologists from different countries have yielded another notable result - the theory of geographic populations of migratory birds as elaborated by professor Isakov and doctor Shevareva. Proceeding from these concepts based on summarized ringing data scholars and practical workers are not trying to elucidate migratory links between individual populations in terms of bird conservation, game management, etc.

The third matter of common concern pertains to the studies of bird passages in terms of environment all conditions and human activities. Such correlations are employed by ornithologists to elaborate a conception of migratory birds as bioindicators of environmental conditions affected by man.

The global population explosion, rapid industrial and agricultural development, exploitation of uninhabited areas in the second half of the 20th century have considerably affected the interrelation between people and birds. In some cases the situation became quite critical.

Increased traffic of both passengers and goods, transported by a sharply growing number of aircraft in the overhead routes used formerly by birds, has resulted in higher rate of collisions. It amounts now to 4,000 per year, thus constituting a priority problem. Radiolocation has acquired great significance as a method of migration investigations and early detection of migratory bird concentrations.

The European Bird Strike Committee (EBSC) acts as a focal point coordinating the efforts of national bodies and organizations along these lines.

The International Waterfowl Research Bureau (IWRB), organized in 1952, has embarked on the programme of management of the most important ecological group of birds. Having summarized the results of the efforts of ornithologists in different countries and birdbanding data for many years, the IWRB elaborated the draft Convention on the conservation of waterfowl habitats, taking ne-

cessary steps for its practical implementation. The Ramsar Convention has provided an excellent instrument for the promotion of nature conservation policy, being based on scientific principles and effectively enforced through concerted action of many nations. The significance of the Convention, making its triumphant march over the planet cannot be too strongly emphasized in terms of protection of birds. The Convention has been presently signed by 30 countries.

It is high time now to undertake studies and practical actions for implementing this Convention, and we address our sincere wishes of success to all our colleagues, working for this noble cause.

Man's contacts with the natural environment occurring in the process of its exploitation, favoured propagation of pathogenic agents of diseases in man and domestic animals by migratory birds and their transport from one part of the globe to another. Ornithologists in conjunction with epidemiologists are now engaged in studying these phenomena. Such studies would be impossible without international co-operation just as in the afore-cited examples.

An active scientific co-operation has already been started. The above problem was discussed at the 1969 and 1976 symposia, held in Novosibirsk on the initiative of Soviet scientists. At present research along these lines is being sponsored by the World Health Organization.

In view of population explosion under conditions of food shortage, migratory birds acquired special significance as crop protectors from pests in addition to pesticides on one hand, and as consumers of agricultural produce on the other.

Although the damage caused by birds to agriculture on a world scale does not exceed several per cent, it is not to be underrated in view of the present-day food shortage.

There is however, hardly any reason for extensive use of toxic substances to annihilate migratory birds, as such an approach is in conflict with the fundamentals of ecology.

It should be remembered that migratory birds constitute an important component of the biocenosis, preventing the reproduction of pests, e.g., the locust, still making its devastating raids and controlled with pesticides at such a high price. Moreover, chemical control, unlike biological, entails an active pollution of the environment.

Thus the discussion of a single problem illustrates how great is the role of international collaboration in the solution of fundamental and practical problems. Various forms of co-operation, employed by international organizations, ensure execution of expanded research programmes, the use of comprehensive approaches, and rational practical application of their results.

The same is true for other problems as well. Opportunities to discuss them will be provided during this congress. We attach particular importance to the activities of various organizations in the development of co-operation. In fact, their efforts have resulted in a network of international bodies to solve - by co-ordinating and making use of the research at national institutions - the most urgent scientific and practical problems, concerning the inte-

rests of all countries. It is my personal belief that this is the most important general outcome of ornithology development over the last decades. This short report was not meant to cover all the aspects of international collaboration. I am aware that my analysis is neither objective nor complete. I have, just intended to emphasize methodological significance of co-operation and its increasing role in the development of ornithology. I should like to conclude my report by paying homage to the memory of Professor Dementyev who did a lot to have us brought together here. He attached great importance to co-operation and foresaw it to be the future of ornithology. Paying tribute to his memory, to the memory of the outstanding scholar and eminent personality, we believe that his words would prove prophetic, and the next generations would recall them as we do.

It is my privilege to welcome you on behalf of the Organizing Committee, to wish you every success in your pursuits.

REPORT OF THE ACTIVITIES OF THE INTERNATIONAL ORNITHOLOGICAL
COMMITTEE AND OF ITS PERMANENT EXECUTIVE COMMITTEE

First Permanent Executive Committee Meeting

The PEC did not meet in the time between the Berlin and Moscow congresses but on one occasion the President of the IOC asked for its advice. The number of permanent appointments for scientists at the Ornithological Department of the Zoological Museum in Copenhagen had been reduced, and the President wrote a letter to the Danish Minister of Education, pointing to the difficult situation which this reduction would create for ornithological research in Denmark and Greenland. Before the letter was dispatched, its contents were communicated to all the members of the PEC for their opinion. All the members, except one, gave their support. The letter did not have the hoped for effect.

The first meeting of the PEC was held at 10 o'clock, August 17, 1982 with President Lars von Haartman presiding and Jurgen Aschoff. Walter Bock, A. Brosset, Valery Ilyichev and Helmut Sick present. Prior to this meeting, the Secretary-General asked Walter Bock to prepare agendas for meetings of the Permanent Executive Committee (PEC) and of the International Ornithological Committee (IOC) and to prepare the reports of these meetings.

After calling the meeting to order, President von Haartman expressed his sorrow at learning of the recent death of Harry Frith who had served the IOC well as Secretary-General of the XVI Congress and as a member of its PEC.

Remarks about the plans and program of the Moscow Congress were made by President von Haartman, Secretary-General Ilyichev and Professor Aschoff, Chairman of the Scientific Program Committee, followed by a discussion and resolution of existing problems.

The question of membership in the IOC was discussed only briefly because insufficient information was available on vacancies in the IOC. A discussion followed on the membership in the IOC (Article I of the By-Laws) and possible modifications, but with no resolution. Formal nominations for new members of the IOC were delayed until the second meeting of the PEC.

Membership in the PEC for 1982-86 was discussed. At the close of the Moscow Congress, Bock, Glutz von Blotzheim and Snow will complete their second term and are ineligible for election. Frith's position became vacant with his death. It was moved, seconded and approved that Aschoff, Brosset, Ilyichev and Sick be nominated for a second term on the PEC. A discussion followed on possible candidates for the remaining positions, but no formal action will be taken until the next meeting of the PEC.

The President expressed his thanks to Professor Aschoff, the designated successor to the elected President in case of force majeure, for his unfailing aid and encouragement throughout the preparations for the Congress. The President had twice asked Professor Aschoff to accept candidature for the presidency of the IOC in the period 1982-86. the first time in 1982, the second at the beginning of the present Congress.

Professor Aschoff had, however, refused.

Two candidates were proposed for president of the XIX Congress, followed by an extensive discussion of the merits of possible candidates. One proposal was withdrawn. Professor Klaus Immelmann (Federal Republic of Germany) was nominated by the PEC as the candidate to present to the IOC.

Possible sites for the XIX Congress in 1986 were discussed. President von Haartman announced that a formal invitation was presented by Canada for a Congress in Ottawa. No other formal invitations had been received prior to the Congress and no additional ones were known. An informal invitation for Spain had been received from a group outside of Spain, but this invitation could not be considered because it was incomplete and because it was not endorsed by a Spanish ornithological group. At this time, Dr. H. Ouellet (Ottawa, Canada), acting as representative of the National Museums of Canada which had extended the invitation to meet in Canada, was asked to address the PEC about details of the invitation and to answer questions. A thorough discussion followed after which Dr. Ouellet was thanked by the committee and asked to make a presentation on the facilities and plans for the Congress(1986) at the second meeting of the IOC. After Dr. Ouellet left, the PEC voted unanimously to recommend acceptance of the Canadian invitation by the IOC.

A short discussion of possible sites of the Congress(1990) followed, but no decision was made.

The PEC discussed the matter of development of new Standing Committees with the members being firmly in favor of formation of additional standing committees, but that the initiative must come from members of the congress interested in a particular committee. It was stressed that any new standing committee should deal with ornithological matters of international scope. During this discussion Professor Ilyichev raised the topic of Applied Ornithology and its relationship to the IOC. Two points were raised. First is that applied ornithology covers a wide range of subjects and that it must be narrowed to be a cohesive, manageable field. Second, the PEC would support very strongly a proposal to form a Standing Committee dealing with international questions of applied ornithology.

Professor Ilyichev announced that a reception was planned for all members of the IOC and their wives at the House of Peace on Friday, August 20, 1982 at 5 o'clock. Some ideas on applied ornithology would be presented by our Soviet hosts followed by a reception. An announcement of this reception would be made at the first IOC meeting.

Aspects of the organization of the IOC were discussed including development of mechanisms for close working relationships with national ornithological societies. No decisions were reached and this matter was referred to future meetings of the IOC.

Bock proposed the need for a mechanism for the formulation of resolutions for presentation to the IOC for their action. He pointed out that a great number of organizations in the USSR had been involved in work to make the Congress successful and that a formal expression of appreciation was needed. It was suggested that the past president be asked to head a committee to formulate resolutions at this and future Congresses. This idea was accepted by the PEC.

President von Haartman will undertake to ask past president Donald Farner if he would accept this task.

Bock also pointed out that more detailed information of the work of the secretaries-general and their local committees would be most valuable to the future secretaries-general in their planning of Congress. Moreover the papers of the presidents, secretaries-general, and other persons associated with this and past Congresses are essential for anyone interested in the history of international ornithology. Almost none of these documents exist from early Congresses, but that it would be possible, with prompt action, to gather the papers of the post-war Congresses and possibly from a few of the pre-war Congresses. Bock proposed that an archives committee be formed which would be responsible for establishing a permanent archive for the IOC and for gathering papers from earlier Congresses. This proposal was accepted unanimously.

The agenda for the first meeting of the IOC was proposed and adopted.

First International Ornithological Committee Meeting

The first meeting of the IOC was held at 19:15 o'clock, August 18, 1982 with President Lars von Haartman presiding.

President von Haartman opened the meeting with an expression of appreciation and cordial thanks to all host organizations, to members of the Soviet Ornithological Committee, to members of all local committees, and especially to Secretary-General Ilyichev, with whom he had fruitful cooperation throughout, for the excellent planning and preparation of the Moscow Ornithological Congress. He also thanked members of the PEC and other committees of the IOC, mentioning especially Professor Aschoff for his brilliant handling of the Scientific Program Committee, members of the SPC and all conveners of symposia for their efforts in arranging a most interesting program, and Professor Bock for his energetic and unselfish work in many aspects of preparation of the congress.

Secretary-General Ilyichev presented some remarks on the program of the congress and post-congress tours. He also announced the reception at the House of Peace for members of the IOC and their spouses on Friday, August 20, 1982 with instructions on how transportation would be arranged.

Professor Aschoff noted that the Scientific Program Committee and conveners of the symposia had already been thanked and that he could not add more to these remarks.

The problem of membership of the IOC was raised and a request was made for information on members who wished to resign or had died. A further request for information on the date of birth of members, including those not present, was made to comply with Article I of the By-Laws.

The president urged the members of the national delegations of the IOC to meet and collect information about (a) members, who had become emeriti since the Berlin Congress, (b) deceased members, (c) members that had not taken part in the two last ornithological Congresses, (d) changes of addresses and also possible changes of citizenship among the members, (e) members wanting

to resign, (f) countries not represented or underrepresented at the IOC and countries that would agree to give up one or more memberships, (g) errors observed in the Berlin list of the IOC. The information should be communicated to the PEC before its following meeting, or at the latest, the next meeting of the IOC.

Invitations for the XIX Congress in 1986 were announced, stating that only one invitation, that from Canada, was available which is a very good one and which has full support of the PEC. Details of this invitation were provided, with some discussion of the proposed date of June 22-29. It was pointed out that this date was selected to avoid as much of the breeding season as possible for those ornithologists doing field work and to still permit pre-congress field trips to various parts of Canada during the breeding season. The invitation to hold the Congress in Ottawa, Canada in 1986 was accepted unanimously and with gratitude, and the Canadian ornithologists and host institution were congratulated on their excellent job in preparing and presenting their invitation to host the XIX Congress.

Professor Finn Salomonson (Denmark) was recognized. He said that the Danish ornithologists would like to hold the Congress(1990) in Copenhagen and said that their work to prepare an invitation would be aided greatly if he could obtain a statement of support from the IOC. He added that such a statement would not constitute a commitment from the IOC to accept an invitation from Denmark.

Dr. R. Liversidge (South Africa) was recognized. He stated that although he has no objections to a future meeting in Copenhagen, he felt that action by the IOC to indicate at this time (1982) that an invitation from Denmark for the Congress(1990) would be considered favorably in 1986 is contrary to tradition of the IOC and to the Statutes and By-Laws adopted in 1978. Positive action by the IOC, Liversidge claimed, would act to discourage activity of other countries which may have been considering development of an invitation for 1990 but had not progressed sufficiently far to present a statement at this meeting. The ensuing discussion indicated that three and possibly four years are required currently for ornithologists from a country to develop the detailed invitation required by the PEC and IOC; both the USSR and Canada started work on their successful invitations four years before they were formally presented and accepted. General agreement existed among members of the IOC that a three to four year lead time was required to develop suitably detailed invitations. This being the case ornithologists should be informed of this necessity and the Statutes (Article II:6) and the By-Laws should be amended to reflect actual practices.

At the close of the discussion on future meetings, President von Haartman asked Professor Salomonson if would be sufficient to have a letter sent from him (or from the president of the XIX congress) expressing interest and support by the IOC for Danish ornithologists in their preparation of an invitation for the XX Congress in 1990 and stating that a formal invitation from Denmark would be seriously considered by the PEC and IOC in 1986. Professor Salomonson stated that such a letter is exactly what he hoped for. President von Haartman asked the members if there were any objections to such

a letter. Hearing none, he stated that it would be sent by him or by his successor.

President von Haartman stated that he received a number of comments by members of the Congress indicating some dissatisfaction with the format of the Berlin and the Moscow Congresses.

He stated that some members felt that the full program of symposia and round table discussions did not permit colleagues to meet in the way possible at earlier Congresses. Also, the arrangement of the scientific program as a series of symposia did not permit private initiative to assert itself. Possibly the symposia, planned several years before the Congress, tend to deal with matters of past importance rather than those of significance in the future. Lastly, he noted that responsibility for the scientific program rests with the Scientific Program Committee which is responsible to the PEC (By-Laws, Article IV:4) and hence ultimately to the whole IOC. He stated that this matter was not discussed by the PEC at their first meeting other than to agree to place it before the IOC for their discussion and recommendations. A free discussion followed by members speaking both for and against the format of the scientific program as evolved in the XVII and XVIII Congresses. A sizable majority of speakers voiced support for the current arrangement, noting that the symposia permitted a strong organization and presentation of subjects of current interest to ornithologists and that poster papers and round table discussions permitted individual ornithologists to present material independently of the decisions of the Scientific Program Committee. A general request was made that symposia conveners and speakers be urged to organize symposia and individual papers to provide reviews of the subject and references to the important literature for the general ornithologist rather than being highly technical presentations directed toward other specialists. The former approach would enhance the primary goal of the congress as a means of exchange of information on diverse aspects of avian biology between workers in many different areas.

President von Haartman informed the IOC of the discussion of the PEC on Standing Committees. Brief reports on the activities of the existing committees were given by Professor K.H.Voous for the Standing Committees for the Coordination of Seabird Research and by Professor W.J.Bock for the Standing Committee on Ornithological Nomenclature. President von Haartman stressed that the PEC and he hoped also the IOC supported strongly formation of additional standing committees dealing with ornithological matters having international scope, but that the initiative for development of any such committees must come from members of the Congress so interested. The IOC would welcome any existing international groups as standing committees, but does not feel that it must serve as the sponsor for all international ornithological agencies. With the interest expressed in applied ornithology at this Congress, it is hoped that these persons would organize a standing committee in this area. It was urged that the chairpersons of standing committees be contacted by the Scientific Program Committee to provide these committees the opportunity to participate fully in the program by developing symposia, round table discussions, etc.

The meeting of the IOC was adjourned until the scheduled second session on August 21, 1982.

Second Permanent Executive Committee Meeting

The second meeting of the PEC was held at 19:15 o'clock August 19, 1982 with President Lars v. Haartman presiding and Jurgen Aschoff, Walter Bock and Valery Ilyichev present. Because of a late announcement of a change in the location of the meeting, the other members of the PEC were unable to attend.

Nominations for members of the PEC for 1982-1986 were open. Walter Bock nominated J. Aschoff (FRG), A. Brosset (France), Valery Ilyichev (USSR) and Helmut Sick (Brazil) for a second term which were accepted without further discussion. A number of candidates were proposed for the remaining positions, with discussion on their merits, on the national distribution of members of the PEC, and on the possible desirability of having a representative from Canada on the PEC in addition to the ex-officio position of the Secretary-General. On the basis of this discussion, the PEC agreed to nominate the following as new members of the PEC for 1982-1986: B.K. Follett (UK), S. Haftorn (Norway), J.R. King (USA) and J.C.R. Rowley (Australia).

Following the action taken at the first meeting of the PEC, Professor Klaus Immelmann (FRG) was nominated by unanimous vote as candidate for the President of the XVII Congress.

Bock proposed Professor Aschoff as designated president for the XIX Congress which was seconded with enthusiasm by von Haartman. Despite protests from Professor Aschoff, he was nominated as candidate for this office.

A discussion followed on nomination of new members of the IOC. Little information was available to the PEC on members who had resigned, died, reached the age of 65 since the XVII congress, or resigned because of absence from the last two congresses (XVII and XVIII). Moreover few names were suggested to the PEC as potential nominees for the IOC. In the absence of sufficient information on current vacancies in the IOC and on potential candidates for membership, the PEC decided, with regret that no further action be taken at this time. The only definite nomination for the IOC made by the PEC is of the nomination of Professor B.K. Follett (UK) to the PEC for 1982-1986.

The PEC reviewed questions referred back to it by the IOC at its first meeting. These questions covered two major points, namely:

a) Modification in the Statutes and By-laws to deal with presentation and consideration of potential invitations to future Congresses.

b) Discussion of the size of the IOC and how members are counted (By-Laws, Article I). Considerable dissatisfaction was expressed on counting members only below the age of 65, on the question of whether past presidents represented their country, on how countries with small ornithological activity are best represented and how to apportion membership according to the ornithological activity of countries (Statutes, Article II: 2).

President von Haartman summarized his views on certain points arising from the Statutes, Articles II: 4 and III: 5 and the By-laws, Article I as follows:

a) Former presidents have, according to the Statutes III: Article 5, been secured permanent membership in the IOC. They are, ipso facto, lifetime members. This implies that a former President remains a member even if he, e.g., for health or economic reasons, can no longer attend the Congresses. If he continues to be a representative of his country, this means that the representation is in fact reduced by one member, this may result in complete lack of representation of small countries.

Former Presidents should, therefore, not be considered representatives of their home country, but should form a special category of the IOC, the permanent members. It might be wise to enlarge this category to include the former Secretaries-General, who have a thorough knowledge of the practical management of the Congresses, and, perhaps, a few other distinguished senior ornithologists.

b) The relation of the emeritus members of the IOC to the representation of their countries (By-laws, Article I) would also have to be reconsidered. If they are not counted as members of the IOC, but counted as representatives of their country, this may cause a de facto reduction of its representation.

Some discussion followed, but it was felt that these matters were too complex to solve by the PEC at its meetings at this Congress. It was recommended that the attention of the President and PEC of the XIX congress be directed to these questions with the recommendation that a committee be appointed to consider them and to recommend any necessary changes in the Statutes and By-Laws in sufficient time that they can be acted on at the XIX congress.

Although the IOC had accepted the invitation from Canada for the XIX congress, the PEC agreed to invite Dr. H.Ouellet (Canada) to make a presentation to the IOC on the facilities in Ottawa and plans for the congress and to answer questions.

The PEC instructed President von Haartman and Secretary-General Ilyichev to confer with Donald Farner on the final wording of resolutions to present to the IOC for adoption.

No unfinished or new business existed for the PEC to consider.

The agenda for the second meeting of the IOC was agreed on.

Second International Ornithological Committee Meeting

The second meeting of the IOC was held at 19:15 o'clock August 21, 1982 with President Lars von Haartman presiding.

Dr. H.Ouellet (Canada) was introduced as the representative of the National Museum of Canada, the host organization for the XIX Congress, and as the nominee for the next Secretary-General. Dr. Ouellet gave an illustrated presentation on the facilities in Ottawa for the next Congress and an overview of the plans. Following his presentation, Dr. Ouellet answered questions and expressed the hope that all members of the IOC will attend the Congress in Ottawa.

The nominations of the PEC for members of the Permanent Executive Committee, 1982-1986, were presented. According to the Statutes (Article IV: 2), members of the IOC were asked if they wished to present additional nominees. None

being offered, nominations were closed. The new PEC consisting of J.Aschoff (FRG), A.Brosset (France), B.K.Follett (UK), S.Haftorn (Norway), V.Ilyichev (USSR), J.R.King (USA), J.C.R.Rowley (Australia) and H.Sick (Brazil) was elected unanimously.

After a short introduction by the President, the IOC discussed ambiguities in the present Statutes and By-Laws with respect to membership in the Committee (compare the meeting of the PEC on August 19). The IOC decided to postpone possible measures until the next Congress.

President von Haartman discussed the difficulties experienced by the PEC in preparing a list of nominees for the IOC. He proposed that the IOC act as a committee of a whole and go through the existing membership of the IOC (as published in the proceedings of the XVII Congress) to determine vacancies and to elect new members. Attention should be given to countries not now represented. The number of vacancies because of death and resignations since the XVII Congress is 14 plus those that opened due to age. The IOC elected 31 new members marked by an asterisk (*) in the list of members of the International Ornithological Committee 1982-1986.

President von Haartman presented Professor Klaus Immelmann (FRG) as the nominee of the PEC for President of the XIX Congress. Professor Immelmann had barely stepped out of the room when he was elected to be a president by acclamation by the IOC.

President von Haartman presented Professor J.Aschoff (FRG) as the nominee of the PEC for designated president of the XIX Congress (Statutes, Article III: 2); he was also elected by acclamation of the IOC.

The recommendation of the PEC for establishment of a permanent archive and for collecting documents from earlier Congresses was presented to the IOC. This idea met with approval of the IOC and a committee consisting of C.Perrins (chairman), P.Berthold, W.J.Bock and D.S.Farner was appointed.

Because Professor D.S.Farner (chairman of the Resolutions Committee) had to leave early, it was not possible to present the proposed resolutions to the IOC for their action. A motion was made and passed that these resolutions be approved by Professors Haartman, Farner, and Ilyichev.

No other unfinished business or new business existing, the IOC adjourned its meetings for the XVIII Congress.

These documents were prepared on the basis of the notes of Prof. Lars von Haartman, Prof. W.Bock and Prof. V.Ilyichev. Prof. K.Immelmann familiarized himself with the manuscript.

Lars von Haartman

Walter Bock

Valery Ilyichev

MEMBERS OF THE PERMANENT EXECUTIVE COMMITTEE 1982-1986 AND
MEMBERS OF THE INTERNATIONAL ORNITHOLOGICAL COMMITTEE 1982-1986

President 1982-1986

Prof. Dr. Klaus Immelmann

Secretary-General 1982-1986

Dr. Henri Ouellet (Canada)

Permanent Executive Committee 1982-1986

Prof. Dr. Jürgen Aschoff

Dr. A. Brosset

Dr. B.K. Follett

Prof. Dr. S. Haftorn

Prof. Dr. Valery Ilyichev

Prof. Dr. James R. King

Dr. J.C.R. Rowley

Prof. Dr. Helmut Sick

International Ornithological Committee 1982-1986

(* newly elected members)

ARGENTINA

Olrog C. Chr. Instituto Miguel Lillo, Universidad Nacional de Tucuman, Tucuman

AUSTRALIA

*Cowling S.J. 123 Brown Street, Heidelberg, Vict.

Rowley J.C.R. CSIRO, Division of Wildlife Research, Clayton Road, Helena Valley, W.A.

Serventy D.L. 27 Everett Street, Nedlands, W.A.

*Schodde R. CSIRO, Division of Wildlife Research, P.O. Box 84, Lyneham, A.C.T. 2602

AUSTRIA

Bauer K. Naturhistorisches Museum, Burgring, P.O. Box 417, A-1014 Wien

Schifter H. Naturhistorisches Museum, P.O. Box 417, A-1014 Wien

BELGIUM

Devillers P.J. Institut royal des Sciences naturelles de Belgique, rue Vautier 31, B-1040 Bruxelles

BRAZIL

Sick H. Museu Nacional, Quina da Boa Vista, Guanabara ZC.08, Rio de Janeiro

BULGARIA

*Nankinov D.N. Institute of Zoology, Sofia 1000

CANADA

*Boag D.A. Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2M7

Erskine A.J. P.O. Box 1327, Sackville, New Brunswick E0A 3C0

Falls J.B. Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1

Gunn W.W.H. P.O. Box 1229, Spruce Grove, Alberta T0E 2C0

Keast A. Department of Biology, Queen's University, Kingston, Ontario K7L 3N6

Richardson W.J. LGL Ltd, Environmental Research Ass., 214 Merton Street, Suite 303, Toronto, Ontario M45 1A6

CHILE

*Schlatter R.P. Instituto de Zoologia, Universidad Austral de Chile,
Casilla 567, Valdivia

CHINA PEOPLE'S REPUBLIC

Cheng Tso-Hsin. Institute of Zoology, Academia Sinica, Haiten, Peking (53)

*Hsu Wei-Shu. Peking Natural History Museum, 126 Tien Chiao Street, Peking(2)

COLOMBIA

Borreiro J.I. Dept. de Biologia, Universidad del Valle, Cali

CZECHOSLOVAKIA

Hudec K. CSAV, Institute of Vertebrate Zoology, 603 65 Brno, Kvetna 8

*Veselovsky Z. Zoological Gardens, 171 00 Praha, 7-Troja 120

CUBA

*Gonzalez H. Instituto de Zoologica, Academia de Ciencias de Cuba, La
Habana 2

DENMARK

Dyck J. Institute of Comparative Anatomy, University of Copenhagen,
Universitetsparken 15, DR-21 00 Copenhagen ø

*Fjeldsa J. Zoological Museum, Universitetsparken 15, DK 2100 Copenhagen ø

Loppenthin P. Torvevej 14, DK-2740 Skovlunde

Salomonsen F. Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen ø
(President, 1969-1970)

EIRE

O'Connor R.J. Zoology Department, University College of North Wales,
Bangor LL57 2UW

EQUADOR

*Ortiz-Crespo F.I. Universidad Catolica del Ecuador, Aptdo 2184, Quito

FINLAND

Frhr. von Haartman L. Åbo, Lemsjöhölm (President, 1978-1982)

*Saurola P. Zoological Museum, Ringing Centre, P. Rautatieck. 13,00100
Helsinki 10

FRANCE

Blondel J. Station Biologique de la Tour du Valat, 13 Sambuc, B.d.Rh.

Brosset A. Museum National d'Histoire Naturelle, Brunoy 91

Dorst J., Museum National d'Histoire naturelle, 55 rue de Buffon, F-75005
Paris 5 (President, 1970-1974)

Erard C. C.R.M.M.O., Museum National d'Histoire Naturelle, 55 rue de Buffon,
F-75005 Paris 5

Etchecopar R.D. C.R.M.M.O., Museum National d'Histoire Naturelle, 55 rue de
Buffon, F-75005 Paris 5

Ferry C. Faculte de Medecine, F-21000 Dijon

Frochot B. Laboratoire d'Ecologie, Universite de Dijon, F-21000 Dijon

Jouanin C. 42 rue Charles Laffitte, F-92200 Neuilly sur Seine

Mougin J.L. Museum National d'Histoire Naturelle, 55 rue de Buffon,
F-75005 Paris 5

Thiolley J.M. 59 rue des Capucines, F-92370 Chaville

FEDERAL REPUBLIC OF GERMANY

Aschoff J. Max-Planck-Institut für Verhaltensphysiologie, 8131 Andechs
Berthold P. Vogelwarte Radolfzell, Schloss, 7760 Radolfzell 16
Goethe F. Institut für Vogelforschung, Kirchreihe 19 b, 2940 Wilhelmshaven
Gwinner E. Max-Planck-Institut für Verhaltensphysiologie, 8131 Andechs
Immelmann K. Abteilung für Verhaltensforschung, Universität Bielefeld
Postfach 8640, 48 Bielefeld
Kuhk R. Schloss Möggingen, 7760 Radolfzell 16
Lohrl H. Edelweiler 73, 7293 Pfalzgrafenweiler 2
*Martens J. Institut für Zoologie, Saarstrasse 21 D-65 Mainz
Meise W. Zoologisches Museum, Papendamm 3, 2 Hamburg 13
Nicolai J. Institut für Vogelforschung, An der Vogelwarte 21, 2940
Wilhelmshaven-Rüstersiel
Schüz E. Elmar-Doch-Strasse 39, 7140 Ludwigsburg
*Wiltshko W. FB Biologie der Universität, Siesmayerstrasse 70, 6000 Frankfurt a.M.
Zink G. Vogelwarte Radolfzell, Schloss, 7760 Radolfzell 16

GERMAN DEMOCRATIC REPUBLIC

Oehme H. Forschungsstelle für Wirbeltierforschung (im Tierpark Berlin)
Am Tierpark 125, DDR-1138 Berlin
Rutschke E. Rosenstrasse 12, DDR-1502 Potsdam-Babelsberg

HUNGARY

Keve A. Madartani Intezet, Kolto Utca 21, Budapest XII

ICELAND

Gardarsson A. Institute of Biology, University of Iceland, Grensasvegur 12,
108 Reykjavik

INDIA

Ali S. 33 Pali Hill Bandra, Bombay 50
Biswas B. Zoological Survey of India, Indian Museum, Calcutta 700016
*Chandola A. Department of Zoology, Banaras Hindu University, Varanasi,
221005

INDONESIA

Somadikarta S. Museum Zoologicum Bogoriense, Bogor, Java

IRAN

Moravej-Hamadani H. P.O. Box 1044, Ahwaz

ISRAEL

Zahavi A. Zoological Institute, University of Tel Aviv, 155 Herzl Street,
Tel Aviv

ITALY

Frugis S., Italian Center of Ornithological Studies, Zool. Institute, Parma
*Papi F. Istituto di Biologia Generale, Via A. Volta 6, 56100 Pisa

JAPAN

Morioka H. Dept. of Zoology, National Science Museum, Hyakunin-Cho 3-23-1,
Shinjuku-ku, Tokyo 160
Nakamura T. Department of Biology, Yamanashi University, Kofu 400

Yamashina Y. Yamashina Institute for Ornithology, 8-14 Nampeidai-machi,
Shibuya-ku, Tokyo

Yoshii M. Bird Migration Research Center, Yamashina Institute for
Ornithology, 8-20 Nampeidai-machi, Shibuya-ku, Tokyo 150

KENYA

*Cunningham-van Someren G.R. Ornithology Department, National Museums,
P.O. Box 40658, Nairobi

Forbes-Watson A.D. c/o VIREO, Academy of Natural Sciences, 19th Street
and the Parkway, Philadelphia, PA 19103

MEXICO

*Ramos M.A. Instituto Nacional de Investigaciones sobre Recursos Bioticos,
Apartado Postal 388, Xalapa, Veracruz

THE NETHERLANDS

Drent R.H. Zoologisch Laboratorium, University of Groningen, Kerklaan 30,
Haren (Gron.)

Mees G.F. Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, 2300 RA Leiden

Pérdeck A.C. Institut voor Oecologisch Onderzoek, Vogeltrekstation, Kemper-
bergerweg 11, Arnhem

Voous K.H. Maasdamlaan 28, Huizen N.H.

NEW ZEALAND

*Bell B.D. Wildlife Service, Department of Internal Affairs, Wellington

*Warham J. Zoology Department, University of Canterbury, Christchurch I

Westerskov K.E. Department of Zoology, University of Otago, Dunedin

NORWAY

Holgersen H. Stavanger Museum, N-4000 Stavanger

Haftorn S. Zoologisk Avdeling, DKNVS, Museet, Erling Skakkes gt. 47 b,
7000 Trondheim

PERU

*Plenge M.A. P.O.Box 2490, Lima 100

PHILIPPINES

Rabor D.S. Museum of Natural Science, Mindanao State University, Marawi City

POLAND

*Pinowski J.K. Institut of Ecology, Polish Academy of Sciences, Dziekanow
Lesny near Warsaw, Lomianki

Tomialojc L. Museum of Natural History, Wroclaw University, U. Sienkiewicza
21, 50-335 Wroclaw

RUMANIA

Vasiliu D.G. Alea Teilor, Bloc 2 C, sc. B 1/4, 0300 Pitesti, 1

SENEGAL

Dupuy A. Parcs nationaux du Senegal, B.P. 37, Tambacounda

*Sylla I.S. Parc national du Djoudj, B.P. 50, Saint-Louis

SOUTH AFRICA

Liversidge R. McGregor Museum, Box 316, Kimberly 8300

Siegfried W.R. Percy Fitzpatrick Institute for African Ornithology,
University of Cape Town, Rondebosch

Winterbottom J.M. 9 Alexandra Avenue, Oranjezicht, Cape Town 8001

SOUTH KOREA

Won Pyong-Oh. Ornithology Institute, Department of Biology, Kyung Hee University, Seoul

SPAIN

Castroviejo J. Estacion Biologica de Donana, Paraguay 1, Sevilla

Herrera C.M. Virgen de la Presentacion 2, Sevilla 1

*Purroy F.J. Museo Nacional de Ciencias Naturales Castellana 84, Madrid (6)

SWEDEN

Curry-Lindahl K. Ministry of Foreign Affairs, Box 16121, 10323 Stockholm 16

Enemar A. Zoological Institute, University of Gothenburg, Gothenburg

Svensson S.E. Ecology Building, Helgonavagen 5, S-22362 Lund

SWITZERLAND

Bruderer B. Schweizerische Vogelwarte, CH-6204 Sempach

Geroudet P. 37 Avenue de Champel, CH-1206 Geneve

Glutz von Blotzheim U. "Eichholzli", CH-6204 Sempach

Schifferli A. Wygart, CH-6204 Sempach

Sutter E. Naturhistorisches Museum, Augustinergasse 2, CH-4051 Basel

UNITED KINGDOM

Burton P.T.K. British Museum (Natural History), Park Street, Tring, Herts.
HP23 6AP

Cramp S. 32 Queen Court, London WC1N 3BB

*Follett B.K. Department of Zoology, University College, Bangor, N.Wales

Fry C.H. Aberdeen University, Zoology Department, Tillydrone Avenue,
Aberdeen AB9 2TN

*Kear J. The Wildfowl Trust, Martin Mere, Burscough, Nr. Ormskirk, Lancs.

Matthews G.V.T. The Wildfowl Trust, Slimbridge, Gloucestershire

Mountfort G. Plovers Meadow, Blackboys, Sussex

Newton I. 12 Hope Terrace, Edinburgh EH9 2AS, Scotland

Nicholson E.M. 13 Upper Cheyn Row, London SW3 5JW

Olney P.J.S. Zoological Society of London, Regent's Park, London NW1 4RY

Perrins C.M. Edward Grey Institute, Department of Zoology, South Parks
Road, Oxford

Snow D.W. British Museum (Natural History), Tring, Herts. HP23 6AP

Tinbergen N. Animal Behavior Research Group, Department of Zoology,
University of Oxford, Parks Road, Oxford (President 1966-1969)

UNITED STATES OF AMERICA

*Balda R.P. Department of Biology, Northern Arizona University, Flagstaff,
AZ 86001

*Baptista L. California Academy of Sciences, Golden Gate Park, San Francisco,
CA 94118

Bock W.J. Department of Biological Sciences, Columbia University, New York,
NY 10027

*Carey C. Department of EPO Biology, University of Colorado, Boulder, CO 80309

Farner D.S. Department of Zoology, University of Washington, Seattle, WA
98105 (President, 1974-1978)

Gill F.B. Academy of Natural Sciences, 19th Street and Parkway, Philadelphia,
PA 19103
Howell Th. Department of Biology, University of California, Los Angeles
CA 90024
*James F.C. Department of Biological Sciences, Florida State University,
Tallahassee, FL 32306
*Johnson N.K. Museum of Vertebrate Zoology, University of California,
Berkeley, CA 94720
King J.R. Department of Zoology, Washington State University, Pullman,
WA 99164
Marler P. Rockefeller University Field Research Center, Tyrrel Road,
Millbrook, NY 12545
Mayr E. Museum of Comparative Zoology, Harvard University, Cambridge,
MA 02138 (President, 1958-1962)
Peterson R.T. 125 Neck Road, Old Lyme, CT 06371
Ripley S.D. Smithsonian Institution, Washington, DC 20560
Short L.L. American Museum of Natural History, 79th Street and Central Park
West, New York, NY 10024
Sibley C.G. Peabody Museum of Natural History, Yale University, New Haven,
CT 06520
Traylor M. Field Museum of Natural History, Roosevelt Road at Lake Shore
Drive, Chicago, IL 60605
Woolfenden G.E. Department of Biology, University of South Florida, Tampa,
FL 33620

UNION OF SOVIET SOCIAL REPUBLICS

Dolnik V.R., Zoological Institute of the USSR Academy of Science, Leningrad
Flint W.E. Institute of Nature Conservation, Znamenskoye-Sadki, 142790.
P.O. Vilar, Moscow Region
*Galushin V.M. Chair of Zoology, Lenin Pedagogical Institute, Kibalchich
Street 6, 129 243 Moscow
Ilyichev V.D. Laboratory of Bird Ecology of the USSR Academy of Sciences,
1st Kotelnicheskyy per., 10, 109 240 Moscow
Isakov Y.A. Institute of Geography of the USSR, Academy
Staromonetny 29, Moscow

Kumari E. Zoological Institute, Academy of Sciences of the Estonian SSR,
Vanemuise 21, Tartu, Estonian SSR

Kurochkin E.N. Paleontology Institute of the USSR Academy of Sciences,
Profsojuznaya ul. 113, 117 321 Moscow

VENEZUELA

Phelps W.H. Coleccion Ornitologica Phelps, Apartado 2009, Caracas 101

YUGOSLAVIA

Matvejev S. ul. Milcinskega 14, 6100 Lyublyana

ZAIRE

De Bont A.F. Walenpotstraat 1 A, B-3060 Bertem, Belgium

ZAMBIA

Dowsett R.J. Nyiko National Park, Private Bag Chilinda, PO Rumphu, Malawi

REPORT OF THE STANDING COMMITTEE ON ORNITHOLOGICAL NOMENCLATURE

The Standing Committee on Ornithological Nomenclature of the International Ornithological Committee is an international body appointed by the President of the latter committee. It serves from the close of one congress to that of the succeeding one. Its functions are advisory on matters of avian nomenclature, and makes recommendations to the International Commission on Zoological Nomenclature on ornithological matters that come before that body. The committee holds a public session during the International Ornithological Congress at which the committee discusses and reaches decisions on matters before it, informs ornithologists of decisions reached earlier, solicits comments and recommendations, and discusses nomenclatural matters of general interest.

A public session of the committee was held in the evening of August 23, 1982 during the Moscow Ornithological Congress with Walter J. Bock presiding and members George Watson and Karel H. Voous present. About 20 members of the congress took part in it.

Tribute was paid to Dr. Eugene Eisenmann, long-time member of this committee and its chairman since the XV Congress (1970) and long-time member of the ICZN, whose death in October 1981 was a sad loss for avian nomenclature and deprived this committee of its most valuable member. Dr. Eisenmann had accepted another term of chairman of this committee with great reluctance because of the press of his duties as chairman of the American Ornithologists' Union Check-list Committee. He finally agreed because of President von Haartman's insistence who stated that Dr. Eisenmann's great experience and his common-sense approach were essential for continued successful work of this committee.

When informed in December 1981 of Dr. Eisenmann's death, President von Haartman asked Walter Bock if he would serve as chairman of this committee. An initial memo was sent to members of the committee on January 20, 1982 and an agenda for the meeting at the Moscow Congress was sent on June, 1982.

In October 1979, the committee was asked for its views on the application by J.P. Hubbard to favor Toxostoma crissale over T. dorsale. Unanimous support for this application was given which was reported at the meeting. Because it was not clear whether this decision was sent to the ICZN, a motion was adopted that this body be so informed.

The status of the name Stercorarius madagascariensis Bonaparte 1857 (see R.K. Brooke, 1981 "What is Stercorarius madagascariensis Bonaparte?" Ardea 69:144) was discussed. General agreement exists that the taxonomy of the large skuas is still insufficiently known, especially at the subspecific level, and that this name should not be allowed to replace the well-known names maccormicki and lonnbergi. Dr. Devillers suggested (in a letter) that the priorities of lonnbergi and of madagascariensis be switched so that the latter name be available in case the population from the Crozets are distinct. Others doubted that this approach was workable under the code and suggested that the name madagascariensis be suppressed under the 50-year rule. A motion was passed that an application be prepared by Drs. Watson and Voous to the ICZN to suppress the name Stercorarius madagascariensis under the provisions of the 50-year rule. /Since the meeting of the SCON in Moscow, it has been learned that use of the name Stercorarius madagarcariensis has already been

advocated by P.A.Clancey, 1982, Durban Museum Novitates XIII(10):132-134 in the combination Catharacta antarctica madagascariensis (Bonaparte), 1857 (? = intercedens Mathews, 1913) = lonnbergi Mathews, 1912. The SCON is concerned with the needless development of confusion stemming from the use of madagascariensis and strongly urges authors and editors not to use this name until an application to the ICZN can be submitted and a decision is reached by that body./

In 1979, Mr. C.W.Benson proposed that a neotype be designated for the species known as Muscicapa ruficauda Swainson, 1838 because the type specimen to which this name is attached is a specimen of Niltava (Cyornis) unicolor Blyth, 1843. The species in question is now known as M.ruficauda Sharpe, 1878. Dr. Wolters objected to this proposal stating that the name M.aequalicauda Blyth, 1851 is available for this species and that the binomer M.ruficauda Swainson, 1838 should be suppressed in favor of Cyornis unicolor Blyth, 1843. Benson answered that the name M.aequalicauda had been used only once in 1930 and that use of aequalicauda in preference to the widely used ruficauda would disturb stability and cause confusion. With the exception of Dr. Devilleres (who in letter agreed with Wolters), the committee agreed with Mr. Benson's application and passed a motion to inform the ICZN of its support for it.

Dr. H.E.Wolters had written to the committee on the possible suppression of three generic names, namely Salicaria Forster, 1827 in favor of the universally used Locustella Kaup, 1829 (Sylviinae), Kelea Merrem, 1818 in favor of Calamodus Kaup, 1829 (Sylviinae) and Callyrhynchus Lesson, 1842 in favor of Sporophila Cabanis, 1844 (Emberizinae). After some discussion, the committee stated that they felt that no major problem may exist in the case of suppression of Kelea in favor of Calamodus as neither name has been used for some time, but they would have no objection to this proposal. A motion was passed that the committee would support Dr. Wolters in an application made to the ICZN to suppress these names and urged him to prepare such an application.

The committee's attention was brought to a forthcoming publication of Dr. Frank J. Sulloway on "The Beagle collections of Darwin's finches (Geospizinae)" which appeared shortly after the close of the congress /September 30, 1982, Bull. British Mus. (Nat. Hist.) Zool. Ser., 43(2):49-94/. Dr. Sulloway (p. 69-70) argues that specimens of Geospiza nebulosa Gould 1837 from Charles Island exist in the collection made by Fitz Roy and hence that the name Geospiza nebulosa has priority over the widely used name Geospiza difficilis Sharpe 1888. Because Dr. Sulloway's paper was not published, the committee was unable to take any formal action, but expressed the strong opinion that changes in names of any species of geospizine finches for purely nomenclatural reasons should be avoided strongly because of the widespread use of these names in the general evolutionary and biological literature. The committee agreed to take up this question again after Dr. Sulloway's paper is published. However, the SCON urges that the name Geospiza difficilis continued to be used for this species until a formal decision is reached.

The committee discussed briefly and agreed in principle to support several applications submitted by Murray D.Bruce and David Holyoak to the ICZN

in 1978, but which had not been published by August 1982, but stated that definite action should be postponed until these proposals are published.

Dr. G.F.Mees (The Netherlands) addressed the committee on a problem in the name Artamus hypoleucus versus A.albiventris (Artamidae) which had been brought to the committee's attention too late to be placed on its agenda. The committee agreed that the name Artamus hypoleucus Sharpe, 1890 was a valid substitution (at that time) for A.albiventris Gould, 1847 for the bird now known as A.cinereus hypoleucus, that albiventer Lesson, 1830 has been used consistently for the Timor population of A.leucorhynchus in the combination with A.leucorhynchus albiventer, that danger of confusion exists between the names albiventris and albiventer, and that the name hypoleucus Sharpe, 1890 should have been preserved under the 50-year rule. The committee agreed further that nothing is gained by the use of albiventris Gould, 1847 as proposed by Storr (1943) and by Ford (1978, *Emu*, 78:105-114), urged Dr. Mees to prepare an application to the ICZN to conserve the name hypoleucus, and passed a motion that they would support such a proposal.

In the efforts of chairman Bock to gather nomenclatural matters to be discussed at the Moscow meeting, several ornithologists complained strongly of long delays by the ICZN and especially by its secretariat in handling applications submitted. It is not uncommon for applications to be unpublished for four to five years after being submitted and in the case of a proposal to conserve the family name Threskiornithidae submitted by Eisenmann, Mayr and Parkes in 1975, eight years have passed without its being published. The committee discussed the extreme slowness of action by the ICZN and the fact that the long delay between submission of an application to final action of the commission and publication of its decision has the potential for confusion in the use of scientific names by ornithologists. The same problem was discussed by the committee at their meeting during the XV Congress in the Hague, 1970 (see p. 13-14 of the proceedings). These delays are especially unfortunate because almost every recent nomenclatural problem in birds could have been solved automatically by the original 50-year rule while now each such case must be submitted to the commission. The members of the committee agreed that the current situation of long delays by the ICZN, especially by its secretariat, was not acceptable and asked the chairman to inform the ICZN and its governing body of its feelings on this matter.

The last item discussed concerned another old problem, which was first discussed at the XIV Congress in Oxford, 1966 (see p. 362-363 of its proceedings), namely a list of family-group names of birds to be placed on the Official List of Family-group Names in Zoology. This action was made necessary by the inclusion of family-group names under the Law of Priority adopted at the XV International Congress of Zoology. Strict use of priority would upset several long-established family-group names in ornithology which could be preserved by application to the ICZN. Although this problem has been discussed at every meeting of this committee beginning at the Oxford Congress, no action was taken because of the enormous and difficult bibliographic task required to determine authorship and publication of family-group names, both those in general use and earlier published but unused names. This task is considered to be a waste of effort, time and money by most members of the SCON. Moreover it is not all certain that clear decisions could be reached

on the earliest use and authorship of many family-group names because these names are not used in a definite and consistent fashion in the earliest literature (i.e., in the early decades of the nineteenth century).

An extensive, but not necessarily complete search for such names was undertaken some years ago by Ernst Mayr with the help of a student - assistant. All of this material was sent to Gene Eisenmann several years ago, but no further work was done. The material is now in the possession of Walter Bock and can be used as the foundation of work made by the SCON in this area.

After a discussion, the committee adopted the following motion:

a) until the committee completes its work and submits an application to the ICZN, all ornithologists are urged to follow current usage as given in Peters' check-list. The committee urges especially that editors of ornithological journals insist on this current usage in papers published in their journals.

b) a small subcommittee of the Standing Committee on Ornithological Nomenclature of 3-4 persons (not necessarily all members of this committee) be established to research family-group names and to prepare a report to be submitted to the SCON at the Congress(1986). This subcommittee shall consist of Walter Bock as chairman and persons appointed by him. It was hoped that G. Mees, G. Watson and H. Wolters would serve on it, and the assistance of other ornithologists would be welcome.

c) the SCON be charged to act on this report at the Congress(1986) and to decide at that time whether to submit an application on family-group names to the ICZN and/or whatever other appropriate action be taken.

Members of the Standing Committee on Ornithological Nomenclature for the periods 1978-1982(XVIII Congress) and 1982-1986(XIX Congress) are as follow (those attending the meeting at the Moscow Congress are marked with an asterisk, *):

Walter J. Bock,* Chairman (1981-1986)
Pierre J. Devillers (1978-1986)
Jean Dorst (1978-1982)
Eugene Eisenmann,* Chairman (1978-1981)
G.F. Mees* (1982-1986)
H. Morioka (1982-1986)
Finn Salomonsen (1978-1986)
Richard Schodde (1982-1986)
David Snow (1978-1982)
L.S. Stepanyan* (1982-1986)
K.H. Voous (1978-1986)
George Watson* (1978-1986)
Hans Wolters (1982-1986)

Respectively submitted for the Standing Committee on Ornithological Nomenclature of the International Ornithological Committee.

Walter J. Bock
Chairman

PLENARY LECTURES

Presidential Address

HAARTMAN L. von

THE BIOLOGICAL SIGNIFICANCE OF THE NUPTIAL PLUMAGE OF THE MALE
PIED FLYCATCHER

KUMARI E.

CONTRIBUTION OF RUSSIAN AND SOVIET ORNITHOLOGISTS TO PALEARCTIC
ZOOGEOGRAPHY

SIBLEY CH.G., AHLQUIST J.E.

THE PHYLOGENY AND CLASSIFICATION OF THE PASSERINE BIRDS, BASED ON
COMPARISONS OF THE GENETIC MATERIAL, DNA

BUSSE P.

GEOGRAPHICAL AND ECOLOGICAL ASPECTS OF BIRD MIGRATION AS A MET-
HODICAL PROBLEM

HAFTORN S.

RECENT RESEARCH ON TITMICE IN NORWAY

IMMELMANN K.

SEXUAL IMPRINTING IN ZEBRA FINCHES – MECHANISMS AND BIOLOGICAL
SIGNIFICANCE

THE BIOLOGICAL SIGNIFICANCE OF THE NUPTIAL PLUMAGE
OF THE MALE PIED FLYCATCHER

Lars von Haartman

Department of Zoology, University of Helsinki, Helsinki 10,
SF-00100, Finland

INTRODUCTION

The nuptial plumage of the male Pied Flycatcher varies more than that of any other passerine bird in N. Europe. It is the merit of the late Prof. Rudolf Drost (1936) to have created a simplified system, whereby to divide the seemingly endlessly variable males into seven types, depending upon the colour of their back:

I. Back completely black.

II. Completely black with the exception of the rump, which is more or less grey-white, grey, or brown.

III. Mainly black.

IV. About as much black as grey or brown.

V. Mainly grey or brown with distinct black, blackish or black-brown spots.

VI. Almost uniformly grey or brown, with small dark spots or tinges.

VII. Uniformly grey or brown.

Males of type VII are very like females. They may or may not have the white spot above the bill, otherwise typical of the male nuptial plumage. In the literature the light-coloured plumage in the male is called Hemmungskleid (repressed plumage).

Drost stressed that the colour should not be determined without catching the bird as, for instance, type IV may look rather dark at a distance, while type VI may seem uniformly light. As the type variation in the males is continuous, the types are, to a certain extent, subjective. Drost's recommendation to use intermediate type (I-II, II-III, etc.) is no real solution, as it only increases the possibilities of making mistakes. In the following text, where published records or (in very few cases) my own notebooks use half-types, I have usually transformed them to the original seven-type system.

From the subjective nature of the types it follows that some care is necessary in using them. Consistency in determining the types can be tested by scoring the same males repeatedly in the same summer, though not in different summers, as the type is not constant throughout the life of the male. For this purpose, I used polygamous males caught at different nest-boxes and only subsequently identified as being the same individual (Table 1). The result is satisfactory, though there were inconsistencies. A closer look at my notes revealed that no less than 6 of the 8 males scored inconsistently were denoted as borderline cases between two types. According to a colourimetric examination (Kniprath, 1965) only one of 15 males in Drost's collection was assigned to a wrong type. Inequivocal proof of identical standards of scoring among different persons is more difficult to obtain, but, for instance, Drost's data on Norwegian and Swedish males and mine on Finnish males tally satisfactorily, though the extreme types were lacking in Drost's relatively small sample.

T a b l e 1. Repeated scoring of colour type of polygamous males in the same year

| | | 1st score, type | | | | | | |
|-----------------|-----|-----------------|----|-----|----|---|----|-----|
| | | I | II | III | IV | V | VI | VII |
| 2nd score, type | I | 3 | | | | | | |
| | II | 2 | 3 | 2 | | | | |
| | III | | 2 | 13 | 1 | | | |
| | IV | | | | 7 | | | |
| | V | | | | 1 | 2 | | |
| | VI | | | | | | 1 | |
| | VII | | | | | | | - |

With the exception of a few studies, the data on nuptial plumage have been obtained from living males. The first investigation of a living population of Pied Flycatchers, that of Trettau and Merkel (1943), was chiefly aimed at clarifying the colour types. One is reminded of the fact that one of the few pre-Mortensenian attempts to mark living birds in nature, that of J.A.Naumann with Buzzards, Buteo buteo, was made in order to check the constancy of the individual colouration in this highly variable species (Stresemann, 1951).

My own studies were carried out at Lemsjöholm, an area of c. 4 sq. km on the coast of SW Finland.

GEOGRAPHICAL VARIATION

Figure 1 shows the main colouration of males in different areas (cp. also Fig. 2). The subsp. semitorquata in North Africa (Curio, 1960) and iberiae in Spain (Mayaud, 1944; Curio, 1960) are dark, though the data are scanty. English males seem to be relatively dark (e.g. Witherby et al., 1949; Curio, 1960). In Dutch (Haverschmidt, 1973) and FRG,GDR (Trettau & Merkel, 1943,1952, Winkel et al., 1970, Zang, 1975) populations dark males are extremely rare or absent. The observations on the population in Silesia (Trettau & Merkel,1943) and Saxony (Creutz, 1950) indicate that the males become darker towards the East. In the USSR, according to Dunajevski (1938), dark males dominate. In the Northern countries, including Denmark (museum specimen investigated by me, excluding males which I considered likely to have been migrants), dark males form about the half of the population.

South of the Swiss-German border, dark males reappear (Eggenberger, 1964; Sternberg, 1964). These populations seem even to exceed the Northern males with respect to the proportion of dark individuals.

The comparison of geographical populations is more stringent if we compare age-classes of males (Fig. 2, 3). These comparisons fully confirm the differences found on comparing entire populations without regard to age. This was to be expected, at the relative sizes of the age-classes should be fairly constant in different areas, owing to the constancy of the clutch size and the general lack of second broods (v. Haartman, 1967b).

The area of FRG,GDR enclave of light males has been given subspecific rank, Ficedula hypoleuca muscipeta. When corresponding age-classes are compared, the overlap of the males belonging to the muscipeta population and those belonging to the nominate population in Switzerland and North Europe is generally about a quarter or less (Table 2).

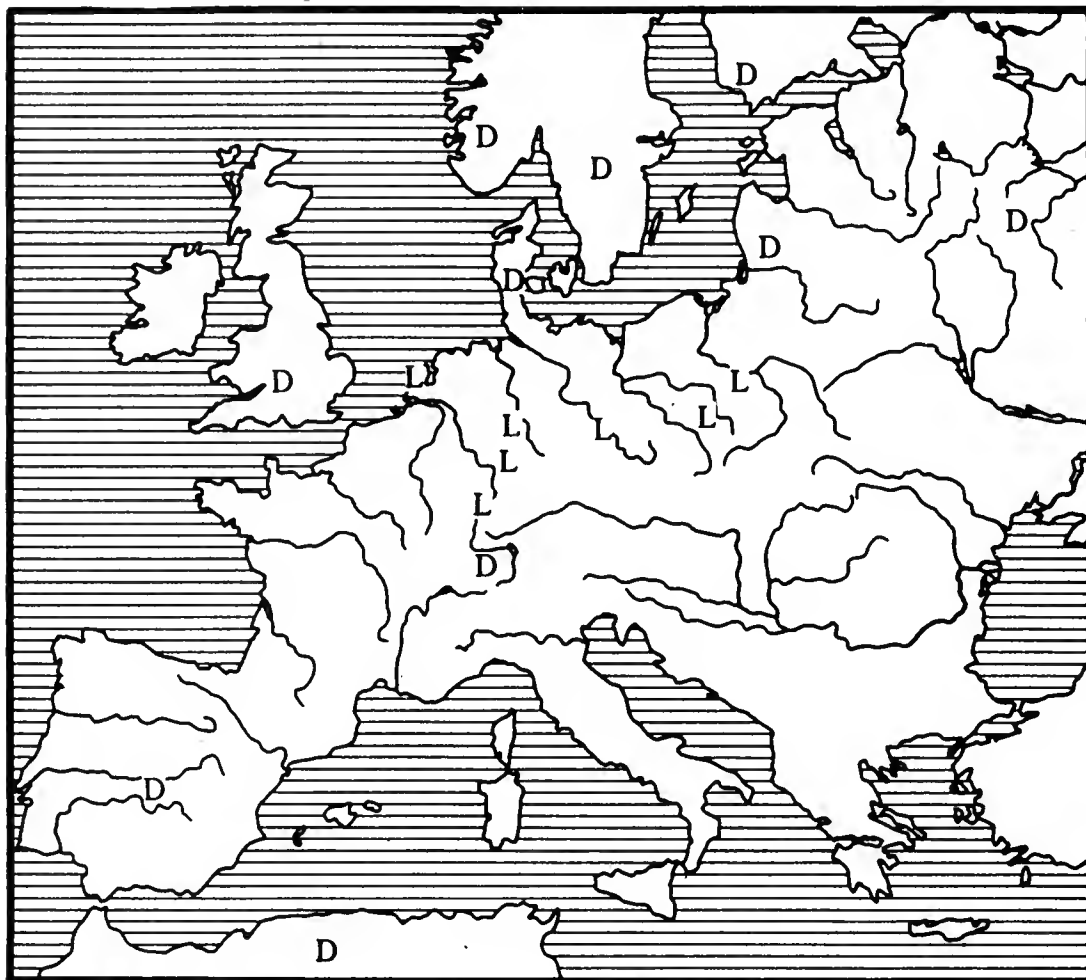


Fig. 1. Colouration of male Pied Flycatchers in the breeding area

L - population mainly light (female-like), D - population mainly dark (data from Creutz, 1950; Curio, 1959, 1960; Drost, 1936; Dunajewski, 1938; Eggenberger, 1964; Haverschmidt, 1973; Mayaud, 1944; Sternberg, 1964; Trettau, 1952; Trettau, Merkel, 1943; Winkel et al., 1970; Zang, 1975; the Zoological Museum of the University in Copenhagen, and my studies at Lemsjöholm)

Table 2. Overlap (percentage) between some North and Central European populations of Pied Flycatcher males with respect to colour types. Age of males 2 yrs. References: cp. Fig. 2

| Norway | | Sweden | | | | | |
|----------|----|---------|---------|---------|-------|----------|--|
| Finland | 79 | Finland | | | | | |
| Denmark | 78 | 64 | Denmark | | | | |
| Holland | 0 | 13 | 18 | Holland | | | |
| Hesse | 0 | 13 | 18 | 67 | Hesse | | |
| Hannover | 4 | 17 | 23 | 95 | 95 | Hannover | |
| Silesia | 15 | 28 | 35 | 60 | 60 | 63 | |

The subspecific rank of muscipeta was denied by Curio (1960) because of an alleged clinal change in colouration, but the evidence of clines is weak. Löhr (1965) holds that the border between h.hypoleuca and h.muscipeta in southernmost FRG, GDR is sharp, the two populations not only occupying different areas, but also different habitats. The transition in Denmark has not been studied closely. East of Central Europe there may be some kind of a cline, but even this is uncertain. What label museum curators put on the diverging GDR population is, finally, of little importance, but for biological purposes it may be useful to maintain the name muscipeta.

On one point the newer data complete the results obtained by Drost (1936). There do exist, although exceptionally, dark males in Central Europe and very

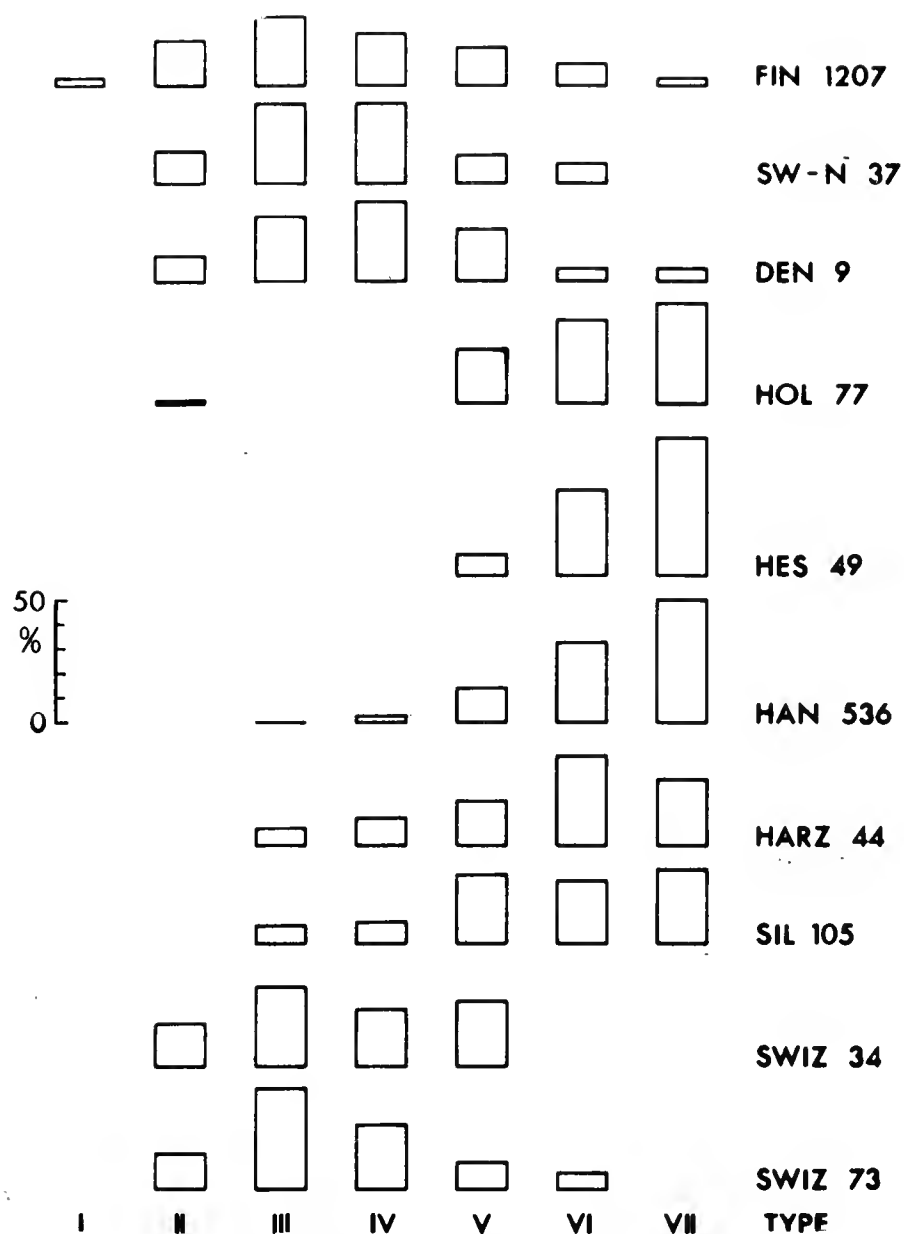


Fig. 2. Colour types of male Pied Flycatcher in Finland, Sweden and Norway, Denmark, Holland, Hesse, Hannover, Harz, Silesia, and two sites, in Switzerland. The figure indicate of male scored (references see Fig.1). For Hannover where the averages did not fit to the figure given, it was assumed that the former were correct

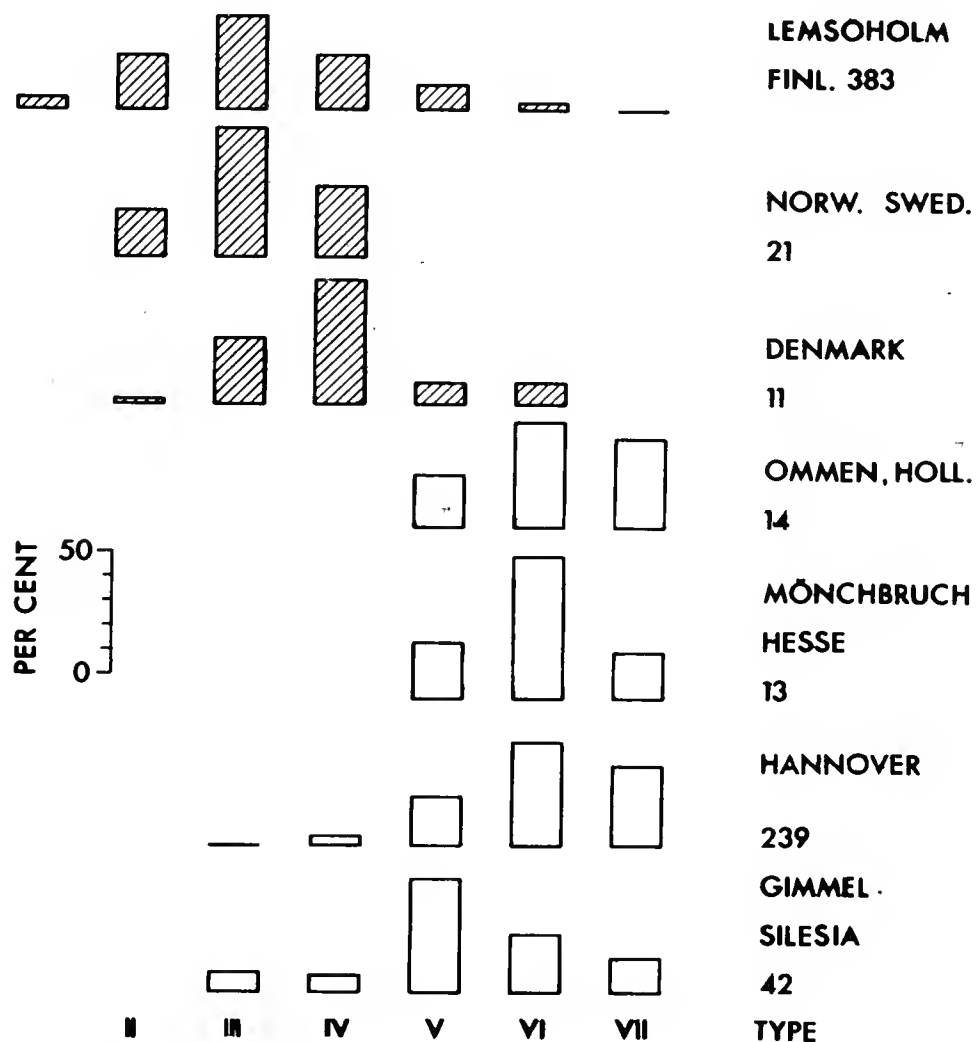


Fig. 3. Colour types of ≥ 2 -yr-old male Pied Flycatchers in Northern and Central Europe (references see Fig.1)

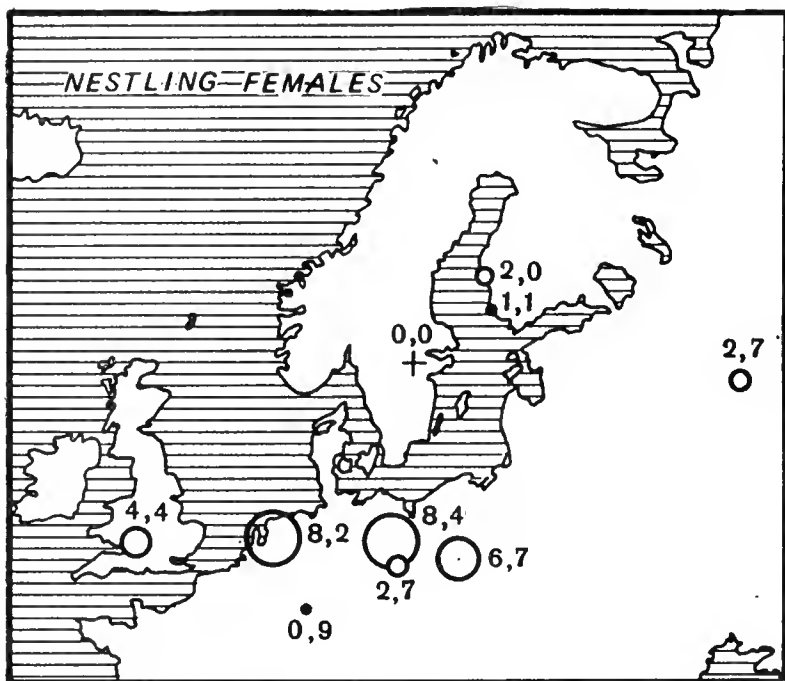


Fig. 4.
Site tenacity, expressed as percentage of individuals recovered, in several study areas in Europe. Female Pied Flycatchers, ringed as nestlings (v. Haartman, 1960)

light males in North Europe. If male colour is determined by polygeny (v. Haartman, 1949), as is the rule with quantitative characters, rare combinations of genes could probably cause the origin of extreme colour types anywhere within the area of the species.

The possible selective factors causing the evolution of the muscipeta type in Holland and FRG, GDR will be discussed later. Suffice it here to say that a prerequisite for the evolution of the Central European enclave of light-coloured males is the strong site-tenacity among the Pied Flycatchers in this region (v. Haartman, 1949, 1960; Fig. 4).

AGE-LINKED COLOUR DIFFERENCES

Drost (1936) and Trettau & Merkel (1943) demonstrated that one-yr-old males are, on an average, lighter than older ones, though there is considerable overlap. This has been confirmed by later studies dealing with the subject. An apparent exception found by Haverschmidt (1973) in Holland may be due to his restricted material.

There may still be some darkening after 2 yrs of age, but it is slighter than that between 1 and 2 yrs (Fig. 5). At greater ages the colouration mainly remains unchanged, though it may vary slightly in an irregular way. The darkening of the plumage before the male's 2nd yr of life is reminiscent of the darkening of the hair in man at the time of sexual maturation and may be connected with the amount of sexual hormones, as well (v. Haartman, 1949).

CONSTANCY OF COLOURATION IN A LOCAL POPULATION

The period during which the colour types of the males was studied at Lemsjöhölm, 1943-81 with only a few years missing, makes it possible to test their constancy. The largest group of males were the immigrants of unknown age (x yrs) settling in the area and breeding. Figure 6 shows the yearly mean of the colour types of these males. There is considerable fluctuation, probably caused by variation in age composition among the immigrants. The overall situation has, however, remained unchanged. The average of the first nine years (1943-1951), 3.77, is very close to the average of the total period, 3.89.

In terms of the human life span this is like comparing man today with man in the Merovingian time.

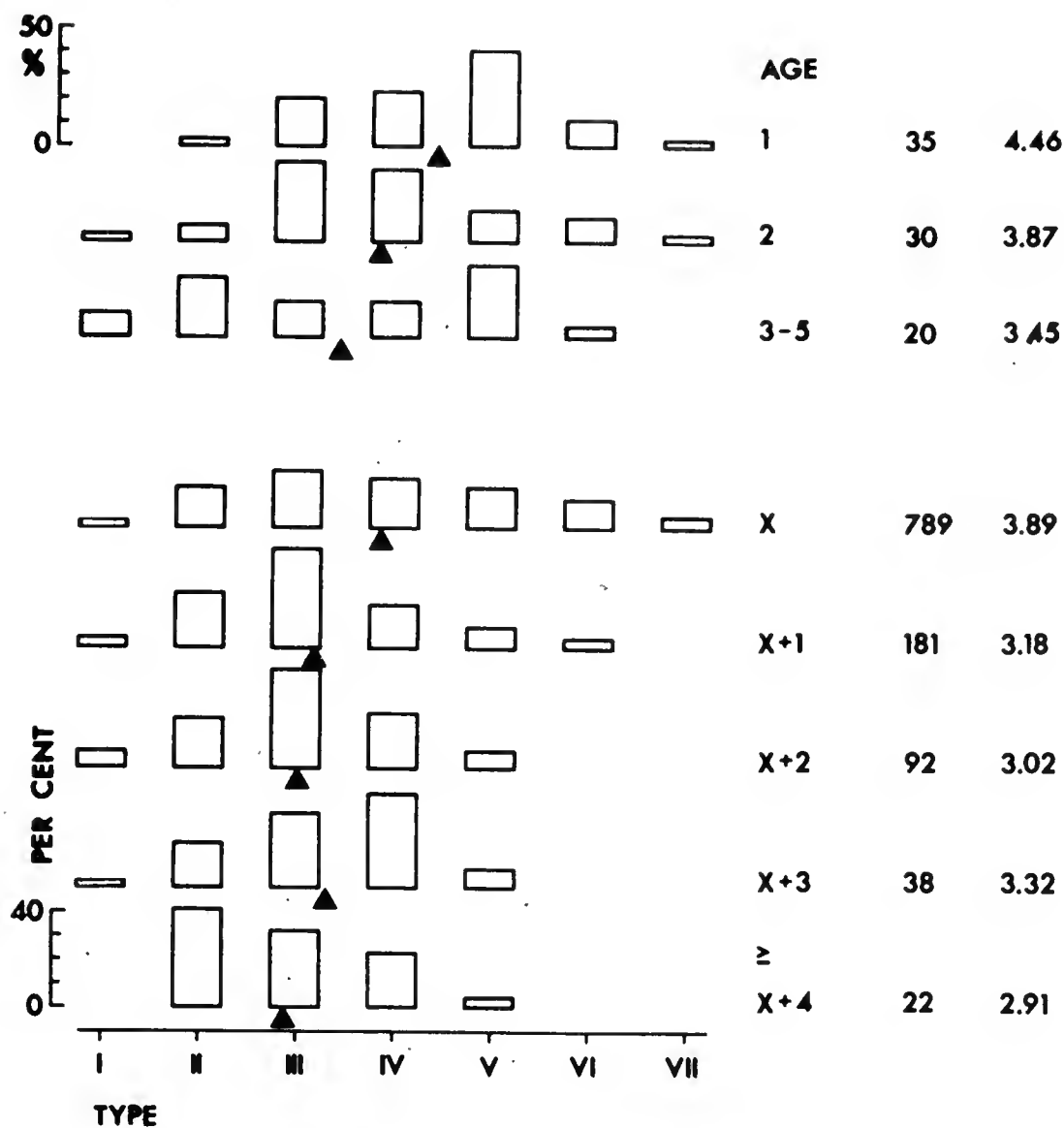


Fig. 5. Colour types of breeding male Pied Flycatchers in relation to age. Observations from Lemsjöholm in SW Finland. The age is given exactly (1, 2, etc. yrs) for individuals ringed as nestlings, and (x, x+1, etc. yrs) for individuals ringed as immigrants. The figures to the right of the age-figures show the numbers of individuals scored, and the figures right of number-figures show the averages, as do also the triangles in the diagram

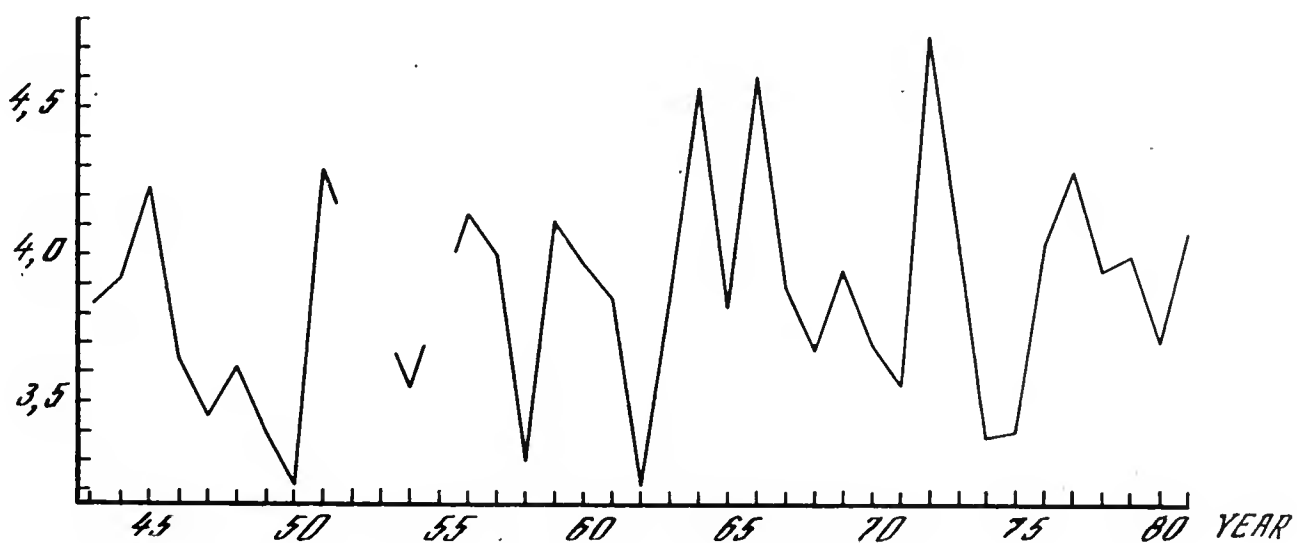


Fig. 6. Average colour type of breeding immigrant (unknown age) male Pied Flycatchers at Lemsjöholm in SW Finland. The average for 1982, not included in the graph, was 3,63

INTERPRETATION OF THE GEOGRAPHICAL VARIATION

In species with sexual dimorphism, the brighter colouration of the male is usually interpreted as the consequence of its courtship and territorial behaviour. The female, who chooses the mate, is herself more camouflaged. The presence of the incubating female is indispensable for the production of offspring, whereas the presence of the male is not. Thus her life during the breeding period is more valuable than his, and this will add to the selection for camouflage in the female.

Obviously, selection for camouflage also occurs in the male, as is demonstrated by the fact that after the breeding season the male Pied Flycatcher moults to a female-type plumage.

The black and white flycatchers, Ficedula hypoleuca and albicollis, form a superspecies, differentiated into two relatively weakly developed sibling species during the ice age(s) when, as shown by Stresemann (1919a, b), Salomonsen (1931), and Voous (1960) European bird populations were easily split up into isolates. The refuge of the Pied Flycatcher was westerly and may well be identified with the Atlanto-Mediterranean refuge in the sense of de Lattin (1967), whereas the Collared Flycatcher may have withdrawn into a southeasterly refuge, perhaps de Lattin's Caspian refuge. Among these flycatchers, the subspecies hypoleuca muscipeta stands out as the only one with mainly greyish-brown males. Further, all seven species, including hypoleuca and albicollis, assigned by Vaurie (1953) to his Ficedula-Siphia group of the genus Ficedula, are described by him as very strongly (5 species) or relatively slightly (2 species, including parva) sexually dimorphic. Against this background, the repressed nuptial plumage of the subspecies muscipeta even more strongly calls for explanation.

The cause does not seem to be climatic. The large population of Pied Flycatchers east and north of the area of muscipeta is dark, thus reversing Gloger's rule.

If we accept that the female-type colouration is cryptic, the following questions arise: (1) is selection for camouflage stronger in the area of muscipeta, (2) why does selection act differently on 1-yr-old and older males?

Among the predators exerting selection pressure for camouflage, the Sparrow Hawk, Accipiter nisus, is likely to play a leading role. L. Tinbergen (1946) studied the predation of Sparrow Hawks upon small passerine birds, though the Pied Flycatcher did not occur in his area. He concluded (p. 202) that "animals which are easily discovered run a great risk". This was already demonstrated by Nordberg (1935) with respect to the choice of prey among migrant Sparrow Hawks at the bird station on Signilskär island (Åland islands). Tinbergen found that Sparrow Hawks hunt where the prey population is dense and in areas that are relatively open and suited to the sneak-and-surprise hunting tactics of the hawk. His conclusion was confirmed by Opdam (1979).

Tinbergen writes that among species laid under heavy contribution by the hawk "about one half or even a greater part of mortality seems to be caused by predation" (p. 206). In the month of May alone, the toll among these species rose, according to Tinbergen, to 5.7-8.4 per cent, according to Opdam to maximally 3 per cent. The selection inflicted by the Sparrow Hawk upon

these species must, at any rate, be evaluated as very strong. Though there are no direct proofs, one may assume that black and white flycatchers males belong among the conspicuous victims of the hawk; the main habitat of the species corresponds to that described above as the most dangerous.

The data available indicate that the density of Sparrow Hawks is higher in Central than in Northern Europe. Below, the three first data concern larger areas, the other data are from areas with a presumably unusually large population. Sources: Mecklenburg and Schleswig, etc. quoted according to Glutz von Blotzheim, Ilmajoki from Sulkava 1964, SW archipelago, Finl. from Aspelund et al., 1982, Kirkkonummi from Forsman 1979, Nauvo from Aspelund et al., Aland from v. Haartman et al. 1963-72, Nijmegen from Opdam 1979, Mittelland, Switzerland quoted according to Glutz, Wytham Wood from Perrins & Geer 1980 (calculated from map).

| | Sparrow Hawk pairs/sq.km | | Sparrow Hawk pairs/sq.km |
|-------------------------|-----------------------------|-------------------------|-----------------------------|
| Mecklenburg | 0.01 | Kirkkonummi, Finland | 0.08 |
| Schl.-Holstein | | Aland | 0.085 |
| + Nordrh.=Westf. | 0.006 | Nijmegen, Holland | 0.1 |
| Finland | 0.003 | Mittelland, Switzerland | 0.1 |
| Ilmajoki, Finland | 0.065 | " maximal | 1.0 |
| SW archipelago, Finland | 0.03 | Wytham Wood, England | 0.06 |
| Nauvo, Finland | 0.08 | | |

The studied Swiss populations of Pied Flycatchers are, it is true, dark, though the Sparrow Hawk population seems to be large. These Swiss Pied Flycatchers are, however, close to the muscipeta population in S. FRG, GDR making gene-flow possible. Generally, there is a certain correlation between the occurrence of the muscipeta colouration in the male Pied Flycatchers and a high density in the Sparrow Hawks. A more definite conclusion will have to be postponed until more is known about hunting by the hawk in the areas where the flycatcher is numerous.

INTERPRETATION OF THE RETARDED ACQUISITION OF FULL NUPTIAL PLUMAGE

In both Ficedula h. hypoleuca and h. muscipeta 1-yr-old males are, on the average, more female-like than are older males. In terms of the present interpretation, they are better camouflaged but less well provided with sexual signals.

The fact that older males, **not** withstanding the selection for camouflage, develop a more conspicuous plumage can only be understood as the consequence of an antagonistic selection pressure, which we may provisionally call sexual selection.

In order to understand the function of the male's nuptial colour, it is necessary to take a look at his behaviour. After arriving in spring, the male searches for a suitable breeding hole. Having found one, he starts to defend it against other males and to attract females to it (Fig.7). When courting a female, he flies to the entrance of the hole, hangs outside it, and jumps in if she approaches. In so doing, he turns his back to the female, repeatedly and for a considerable time. Also, if not followed by the female after jumping into the hole, he sits in the entrance looking out, showing his head and the white



F i g. 7. Nest-demonstration by the male Pied Flycatcher, the female to the left. (from v. Haartman, 1951a)



F i g. 8. Nest-demonstration by the male Pied Flycatcher; the male looks to the right for the female (photo v. Haartman)



F i g. 9. Pied Flycatcher at the nest-box

spot on his forehead. The main function of the colour of the back and the forehead is, obviously, to enhance the nest-hole demonstration (Fig. 8 from v. Haartman, Löhr1, 1950).

The white breast of the male has another function, which is mainly shown in territorial conflicts. The territory owner turns and faces the intruder with raised breast feathers, so that he looks enormously enlarged. He also raises the feathers on his back, especially those on the rump, but because of his frontal orientation, this is of minor importance. (Fig. 9).

Males may attack crude models made of white feathers. But they do so very irregularly and only near the nest hole, and this experiment actually tells us rather little. The function of the white breast cannot be to evoke attack

in other males, but to intimidate them (cp. the experiments by Radesater, Fernö, 1979 with Cichlasoma meeki).

If the colour of the back serves to enhance the male's nest demonstration, and if other reasons than their colour reduce the chance of the young males' marrying, it may be profitable for them to postpone development of full nuptial colour. This may make them less vulnerable to predators and more likely to survive to produce offspring later.

FAILURE TO MATE IN 1-YR-OLD MALES

In an earlier study (v. Haartman, 1949, 1951b) I estimated the number of unmated males at $1/3-1/2$ of the total. This estimation was based on an attempt to catch unmated males holding territories in my study area. The method is not very exact, since it involves the following sources of error: (1) because of polyterritorialism, a seemingly unmated male holding a territory in the study area may be mated somewhere else, (2) as young males often hold territories for only a short time, they may escape observation, (3) it is by no means certain that all young males hold territories.

Instead, one may use alternative methods, of which I have been fully aware since the 1940's, but which demand data not available at that time.

(1) Let N_1 be the number of 1-yr-old males, including non-breeders, N_2 the number of 2-yr-old males, $N_{(x+1)}$ the number of males of the age $x+1$ (males in the year after they were ringed as adults of unknown age), and $N_{(x+2)}$ the number of males of the age $x+2$. Further, let n_o be the number of non-breeding, and n_b the number of breeding 1-yr-old males. Then: $\frac{N_1}{N_2} = \frac{N_{(x+1)}}{N_{(x+2)}}$. As

$N_1 = n_b + n_o$, we will get $n_o = N_2 \frac{N_{(x+1)}}{N_{(x+2)}} - n_b$. Inserting the values $N_{(x+1)}=266$, $N_{(x+2)}=112$, $N_2=35$, and $n_b=39$, we will get $N_1=83$, and $n_o=44=0.53$ (or 53%) of the 1-yr-old males. I call this and similar methods a method of analogy.

(2) Another analogy method uses partly the same values. Let N_1 be the number of 1-yr-old males, n_b be the number of breeding 1-yr-old males, n_o the number of non-breeding 1-yr-old males, n_2 the number of 2-yr-old males that did not breed at 1 yr of age, $N_{(x+1)}$ the number of $(x+1)$ -yr-old, and $N_{(x+2)}$ the number of $(x+2)$ -yr-old males. Then: $\frac{n_o}{n_2} = \frac{N_{(x+1)}}{N_{(x+2)}}$, and $n_o = n_2 \frac{N_{(x+1)}}{N_{(x+2)}}$. Finally, $N_1 = n_b + n_o$. Using the figures given under (1), and $n_2=23$, we find that $n_o=0.59$ (or 59% of N_1).

(3) A third method available is based on a different principle. I call it the method of the young lab assistant, as the central method is the same as mixing alcohol of two different concentrations in order to get a third concentration.

In a ringed population of breeding individuals there will be n_1 individuals known to be 1 yr old, n_2 known to be ≥ 2 yrs old, and n_x immigrants of unknown age. Let $n_x = a + b$, where a is 1-yr-old, and $b \geq 2$ -yr-old birds. Further, let t_1 be an average quantitative characteristic of n_2 , and t_x the corresponding characteristic of n_x . Then: $t_1 a + t_2 b = t_x n_x$. Substituting for b the expression $n_x - a$, we get $a = \frac{n_x(t_x - t_2)}{t_1 - t_2}$, and the total number of breeding 1-yr-old males is $A = n_1 + n_x \frac{t_x - t_2}{t_1 - t_2}$.

Assuming that all ≥ 2 -yr-old birds breed (which is not quite true) and

Table 3. Average colour types and polygamy frequencies in male Pied Flycatchers in my study area.

| Average colour type | | Average polygamy frequency | |
|---------------------|-------------|----------------------------|-------------|
| $t_1 = 4.47$ | $n_1 = 36$ | $t_1 = 0$ | $n_1 = 40$ |
| $t_2 = 3.21$ | $n_2 = 383$ | $t_2 = 12.1$ | $n_2 = 495$ |
| $t_x = 3.91$ | $n_x = 789$ | $t_x = 6.5$ | $n_x = 738$ |

that the survival rate (s) is age-independent (which seems to hold true, at least to an advanced age), the total number of 1-yr-old males is $1-s$, and of all ≥ 2 -yr-old males = s . The number of non-breeding 1-yr-old males is consequently $1-s-A$.

As t -values all kinds of morphological or physiological differences between younger and older individuals may be used, as colour type, wing length (Creutz, 1950; Löhrl, 1954; Alatalo et al., 1981), polygamy frequency, arrival date, laying date, and clutch size.

The following t and n values were established in my study area (Table 3).

Using the average colour types it follows that among the 789 n_x individuals 439 were (a) 1-yr-old, and (b) 350 ≥ 2 -yr-old. In all, there will be 475 breeding 1-yr-old, and 733 ≥ 2 -yr-old males. As the survival rate is c. 0.5 (v. Haartman 1951b), the number of non-breeding 1-yr-old males is $733 - 475 = 258 = 0.35$. If there are 10 per cent unmated males among the ≥ 2 -yr-olds, as assumed by Curio 1959, the proportion of unmated 1-yr-old males will be $= 805 - 475 = 331 = 0.41$.

Using the polygamy frequencies as t -values gives the proportion of unmated males of 1 yr of age = 0.56.

In summary, these methods fail to give an unequivocal result with respect to the proportion of unmated 1-yr-old males. The reason is clear. Some of the figures upon which the calculation has to be based are too small to give reliable averages. Other figures are otherwise open to question, e.g. the annual survival rate. As the results have been relatively close to the proportion 0.5, being (1) 0.53, (2) 0.58, (3) 0.35, corrected to 0.41, and (4) 0.56, we may assume the proportion to be about 0.5, but, perhaps, as high as 0.6.

Instead of using average colour types, one could use the entire distribution of the types within the age classes in question. This improvement would, however, be more apparent than real, as it would not mend the sources of error involved in the calculation.

The uncertainty with respect to the numbers of unmated individuals will continue to complicate our models of the population dynamics of the Pied Flycatcher. For the present purpose, however, it is important to establish that the chances of marrying are severely reduced among 1-yr-old males.

FAILURE TO MATE IN 1-YR-OLD FEMALES

Analogous methods indicate strongly that there is a considerable proportion of non-breeding 1-yr-old females. A small but representative sample of ringed Pied Flycatchers returning to an area in S.Hesse may serve as an example (Table 4).

T a b l e 4. Numbers of Pied Flycatchers returning to an area in S.Hesse (Lambert, 1957)

| Status when ringed | Sex | Yrs after ringing | | | | |
|--------------------|--------|-------------------|----|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 |
| Nestlings | Male | 8 | 10 | 2 | 1 | - |
| Nestlings | Female | 13 | 16 | 5 | 3 | 1 |
| Adult x yrs | Male | 6 | 2 | 2 | - | - |
| Adult x yrs | Female | 11 | 6 | 2 | 1 | - |

As we see, both males and females delay their breeding. Further, in both sexes the proportion not breeding till the age of 2 yrs seems to be larger than the proportion breeding at the age of only 1 yr.

Silverin (1975) found females without a breeding spot in the midst of the breeding season. Using the method of quantitative characteristics (average breeding time, average clutch size), information may be obtained about the age of the females at first breeding. If all females bred at 1 yr of age, and only half of the males, there would be a great surplus of breeding females and male polygamy would have to be much more common.

The nearest we can come to knowledge of the sex ratio in adult Pied Flycatchers is, perhaps, the numbers of both sexes established by catching at ringing stations. In the springs of 1973-80, 1125 Pied Flycatchers were caught and sexed (38 individuals were not sexed) at the bird stations on Lågskär (SW Aland Islands) and Rönnskär (SW Helsinki). Of them 45%±1.48 were males, 55% females. The difference, though small, is highly significant, but may well have some such explanation as longer rests on the islands among the females. On the bird station on Helgoland the same proportion (463 sexed, 46% males, Bub et al., 1981) was found. Silverin (1975) found 48% of the nestlings to be females, 52% to be males. The difference was not significant.

DELAYED BREEDING AGE IN SMALL PASSERINES

The large proportion of unmated individuals in the Pied Flycatcher may easily be understood if we consider its way of nesting. Hole-nesters breed generally much more successfully than do birds breeding in open nests (Nice, 1957, confirmed by numerous later studies). Undoubtedly, many more passerine species would breed in holes, if these were available in unlimited number. But this is not the case, and the lack of sufficient holes will affect the late breeding species in particular. "The early bird gets the worm" - and the nesting hole (v. Haartman, 1968). For the late ones there will be too few opportunities to breed in holes (cp. Fig.10).

The way in which late breeding hole-nesters like the Pied Flycatcher have adapted to this situation is probably that the presumptive losers, the younger individuals or some of them, do not engage very seriously in the competition for breeding opportunities. Regression of the nuptial plumage is the most conspicuous, but probably not the only one of the restraints.

An even more extreme situation was found among North European Starlings, Sturnus vulgaris; no males and few females breed at the age of 1 year (Berthold, 1964). In the Goldeneye all 1-yr-old individuals are assumed to refrain from breeding (v.Haartman, 1981). In the open-breeding Tufted Duck,

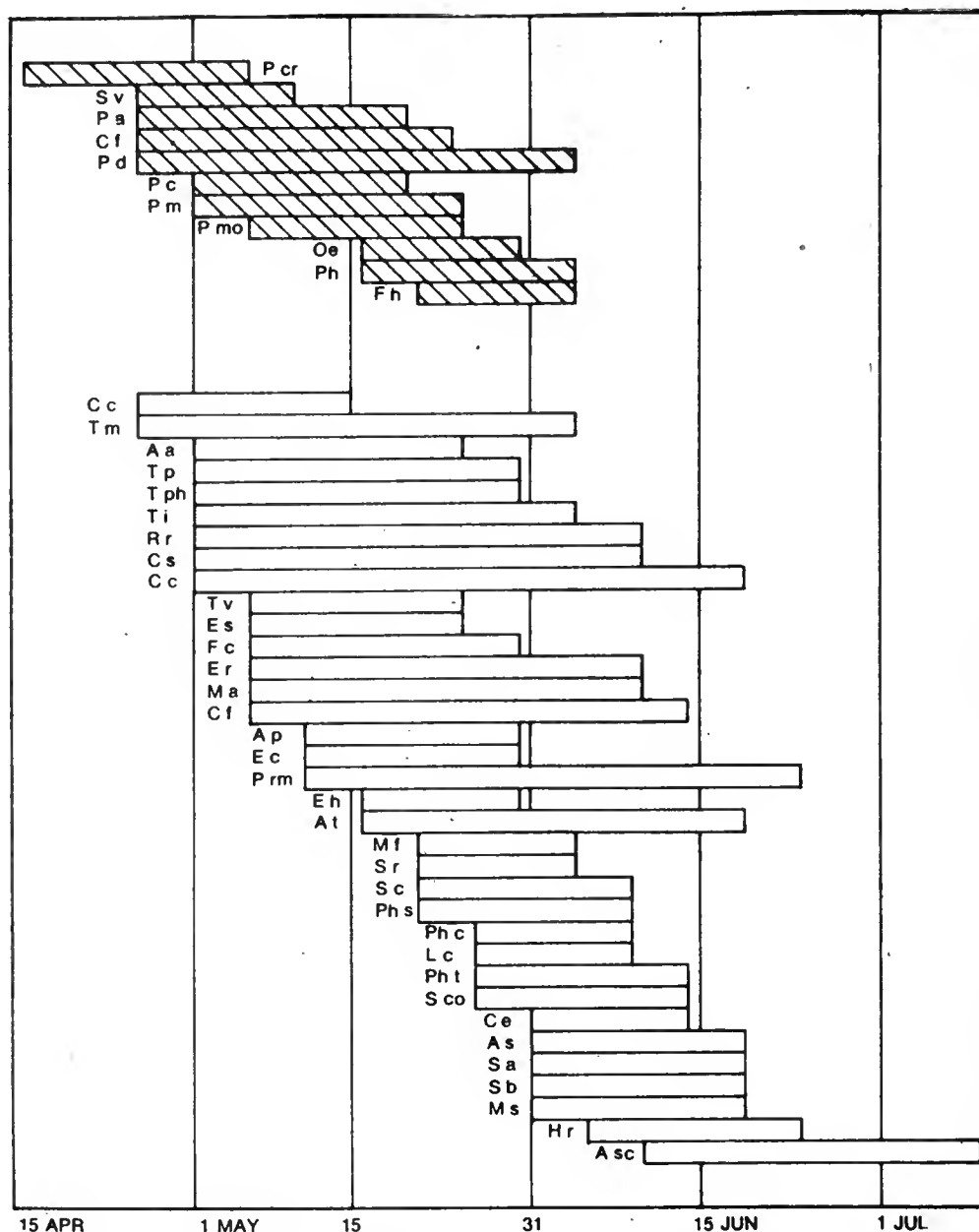


Fig. 10. The laying periods of small passerine birds in South Finland. The beginning and end of the main periods are indicated. Hatched - hole-breeding species, non-hatched - open-breeding species. The scientific names of the species are indicated by the first letter (s) of the genus and species names (e.g. Ficedula hypoleuca - F.h), or by the genus name alone, if identical with the species name (e.g. Phoenicurus phoenicurus - Ph). For further information see text. Note the lack of late-breeding hole-breeders (v.Haartman, 1968)

Aythya fuligula, a diving duck of the same size, practically all individuals seem to breed.

In a population of Red-breasted Flycatchers, Ficedula parva, Müller found 6 unmated out of 26 males. Only one of them had a red-throat, whereas 8 out of 12 mated males were red-throated, indicating that the majority of the non-breeding males were 1-yr-old and/or that the nuptial plumage played a considerable role in the mating.

In species with open nests the territorial system may well force part of the birds to refrain from breeding (Carric, 1963; v.Haartman, 1972) or breed in inferior habitats. These conclusions are supported by the cases where rash successors promptly appeared to fill territories where the previous owner had been caught or shot (Darwin, 1971), and also by the enormous increase in the population density of many species after the improvement in breeding opportunities, as in the excellent experiments carried out by the late Sebastian Pfeifer (1953; 1963).

THE POLYGAMY OF THE PIED FLYCATCHER

The sequence of events leading to male polygamy in the Pied Flycatcher has been described in detail earlier (v. Haartman, 1945, 1951a, 1956a, 1969a). Those earlier studies were based on colourringed individuals. Later, the vast majority of my birds carried only aluminium rings, which may have caused some cases of polygamy to be overlooked. The following quantitative data may, therefore, be considered minimum values.

Males tend to arrive earlier than females, though there is considerable overlap (observations on Pied Flycatchers caught and ringed at ringing stations off the coast). As soon as he has found a suitable hole, the male starts to sing and claim a small territory, centred around this hole. Foreign males are driven off, and the approach of a female releases the male's nest demonstration, described earlier.

In the case of the first nest building takes 6-11 days, on an average 8.3 days (Stjernberg, 1974). From c. 5 days before the female lays her first egg, copulations occur. At the time when the female lays her first egg, sometimes one or two days before, the male disappears for shorter or longer periods, searching for a new territory. The majority, though not all males, behave in this way, i.e. make an attempt to become polygamous, though the proportion of the males to manage it is small.

If the male has found a second nest hole, he starts his territorial behaviour anew. His chances of obtaining a new female are, however, not particularly good. By now it is usually rather late in the season, and few females seem willing to mate any more. If the male does not secure a second female, he will return to his incubating mate, to feed her and help to raise the young, when hatched. If he manages to obtain a second female, he will normally return to his first mate at the time when the second starts to lay, though in exceptional cases he may try his luck at a third nest hole and even marry a third female.

The male mainly aids his first female and first brood, but, after finishing his work with the first brood, may return to his second one, helping to feed the young. He may also alternate between the two territories, but in all the cases I have studied, he was more attentive to the first brood.

The first and second breeding territories of a male are often at a considerable distance from each other, sometimes as much as a whole kilometre apart.

The polygamy of the male is generally what I have called successive and polyterritorial (Table 5). Exceptions occur when the male claims territories around **adjacent** nest holes and manages to obtain a female almost simul-

T a b l e 5. Polygamy frequency in the Pied Flycatcher in its relation to the age of the male.

| Age of male | Monogamous | Polygamous | Percentage |
|-------------|------------|------------|------------|
| 1 yr | 40 | - | - |
| x yrs | 690 | 48 | 6.5 |
| ≥ 2 yrs | 50 | 7 | 12.3 |
| ≥ x+1 yrs | 385 | 53 | 12.1 |
| | 1165 | 108 | 8.5 |

taneously in both. As shown earlier (v. Haartman, 1951) polygamy is age-cor-related. More recent studies gave the following proportions of polygamous males.

As shown in paragraph 7 about 1/2 of the x-yr-old males are 1 yr old. This is probably the reason why the frequency of polygamy among these males is c. half that among old males.

THE ROLE OF THE NUPTIAL PLUMAGE IN 1-YR-OLD MALES

As polyandry does not occur in 1-yr-old males (or, if occurring, is very rare), this is obviously not the factor selecting for nuptial colours in these young males. Instead, it may be the chance to mate monogamously, as opposed to not mating at all, which promotes the evolution of a modest nuptial colouration in 1-yr-old males.

Non-breeding 1-yr-old males cannot be caught and compared with the breeding ones, which would be the natural way to discover differences existing between them. Instead, we have to devise a roundabout method to solve the problem. It is known that there is a certain constancy in the male plumage, so that (relatively) dark 1-yr-old males are also dark at 2 yrs of age, and light 1-yr-old males remain light (Table 6).

T a b l e 6. Darkening of the male's nuptial plumage from the 1st to the 2nd yr of age

| Colour type, 2 yrs of age | Colour type, 1 yr of age | | | | | | |
|---------------------------|--------------------------|----|-----|----|---|----|-----|
| | I | II | III | IV | Y | YI | YII |
| I | | | | | | | |
| II | | | 1 | | | | |
| III | | | 1 | 1 | 1 | | |
| IV | | | | 2 | 1 | 1 | 1 |
| Y | | | | | | 1 | |
| YI | | | | | | | |
| YII | | | | | | | |

The colours of 2-yr-old males will therefore give a clue to their colours the year before (Table 6).

T a b l e 6a. Colour types of males that (1) bred at the age of 1 yr, (2) bred only at the age of 2 yrs

| | Colour type at 2 yrs of age | | | | | | | | |
|-----|-----------------------------|----|-----|----|---|----|-----|----|------|
| | I | II | III | IV | V | VI | VII | N | M |
| (1) | - | 2 | 3 | 5 | 1 | - | - | 11 | 3.45 |
| (2) | 1 | 1 | 7 | 4 | 3 | 3 | 1 | 20 | 4.00 |

There is an indication that those males that were darker at the age of 1 yr were more successful in mating. In the light of the following paragraph this indication is very plausible.

POLYGAMY AND NUPTIAL PLUMAGE IN OLDER MALES

In males older than 1 yr, lack of success in obtaining a mate is rare. Though not very common, either, polyandry would probably be common enough to promote the evolution of a dark nuptial plumage, if this is preferred by the female.

T a b l e 7. Correlation between polygamy and colour type in ≥ 2 -yr-old m males of the Pied Flycatcher

| | Colour type | | | | | | |
|----------------|-------------|------|------|-----------|-----|-------------|-----|
| | I | II | III | IV | V | VI | VII |
| Monogamous | 13 | 65 | 113 | 69 | 25 | 7 | - |
| Polygamous | 1 | 12.5 | 19.5 | 6 | 1 | 1 | - |
| Percentage | 7.1 | 16.1 | 14.7 | 8.0 | 3.9 | 12.5 | - |
| 33/224 = 14.7% | | | | 6/75=8.0% | | 2/34 = 5.9% | |

Considerable difficulties are encountered in studying female preference. At the first glance, the situation may seem simple. One-yr-old males - repressed nuptial plumage - no polygamy - half of the males failing to mate. Older males - nuptial plumage fully developed - unmated males rare - polygamy occurring. But the main cause of the difference in mating success between 1-yr-old males and older ones may be behavioural rather than connected with the plumage, and so, in order to establish the role of colouration, we have to compare the males of the same age-class with each other.

The x-yr-old males are a compound age class, consisting of 1-yr-old and older males. These males cannot, therefore, be used to test the correlation between polygamy and nuptial colouration. Instead, it seems safe to use males, known to be ≥ 2 yrs old. In the following table, which is central to the theme of this treatise, I have retained the original classification of males in half-types, which I, unfortunately, sometimes used in the 1940's (Table 7).

The correlation between polygamy and colour type in the male is highly significant. It holds true with all classes of colouration, except those in which the number of individuals is very small (types I and VI). Polygamy was 2.5 times as common in dark as in light-coloured males.

It ought, perhaps, to be added that the seemingly mediocre success of the males of type I may reflect a true situation. Though darkest, these males lacking a light rump, show in fact less contrast, as seen from behind, than males of the types II and III.

THE CHOICE OF MATE BY THE FEMALE

When choosing her mate, the female Pied Flycatcher should use a number of criteria in order to maximize her reproductive success. The following list may not be complete, but illustrates the female's situation:

(1) Necessity of a swift choice. Clutch size in the Pied Flycatcher is determined by the date of laying; the earlier the laying, the larger the clutch (v. Haartman, 1951b, 1967a, b, and under print). The female possesses a built-in taximeter which starts to run on the first possible day of breeding. The cost of postponing breeding by a single day averages 0.07 eggs (v. Haartman, 1967a). With a mean clutch size of 6.3, this equals a negative selection per day of retardation of 0.011. In fact, her loss is larger than this, since (1) the survival of fledged young to maturity is nearly three times as high in early as in late broods (Table 8), and (2) late broods, if lost, are likely to have a smaller chance of being renewed.

(2) Nest hole of male. The nest hole should protect the offspring against enemies, cold and moisture. This implies that the entrance should be as narrow as possible, not admitting birds larger than a flycatcher. It should be dark, so that a predator perching in the entrance should not discover its contents. There are indications that the female's choice is influenced by these factors (summary in v. Haartman, 1971).

(3) Habitat. The terrain around the nest hole should provide food not only for the pair at the moment of settling, but also for the nestlings one to one and a half months later (nest-building c. 8 days, Stjernberg, 1974, egg-laying 6 days, incubation 14 days, v. Haartman, 1956 c). Askenmo (1977) presents evidence that the habitat affects the female's choice, but it obviously cannot be an easy task for the female to produce a swift and reliable forecast of this kind. Would an entomologist be able to do it? The food supply in the habitat ceases to be a problem as the young fledge, as they immediately leave the territory.

(4) Avoidance of polygamists. Second females usually receive a reduced share of co-operation, as the male mainly feeds his first brood, turning to the second one when his first young are fledged. American sociobiologists (Verner, 1964; Verner and Willson, 1969; Willson, 1966; Orians, 1969; Wittenberg, 1981) assume that some males possess such valuable real estate that, in spite of reduced aid, it pays to marry one of them rather than one of the unmated males ("polygamy threshold"). This hypothesis will be discussed further. Suffice it here to repeat the comment upon point (3) with respect to the difficulty of weighing presumptive territory qualities against each other.

(5) Male nuptial plumage. Unless this brings some compensating advantage, the female should avoid marrying a male so brightly coloured that he risks being killed by a predator before he has fulfilled his duties as paterfamilias. This is a central problem in sexual selection and will be discussed further.

(6) Age of male. Experienced males should be preferred. One-yr-old females lay small clutches (v. Haartman, 1967a), which indicates that their ability to find food is poor. One-yr-old males are likely to show a similar lack of efficiency.

(7) Repeat clutches. If she loses her clutch the female should remarry in a territory at some distance from the first. The main cause of early losses is the Wryneck, Jynx torquilla (v. Haartman, 1957) and during their courtship period Wrynecks will go on clearing out nest holes in an area of considerable size. In fact, the Pied Flycatcher female nearly always leaves her mate and the area where she lost the clutch. This exemplifies how finely adapted her choice may be if conditions allow.

The real estate threshold hypothesis for polygamy seems theoretically sound, but as Goethe said, every theory is grey, and only life is green. Since my earlier papers on polygyny in the Pied Flycatcher (e.g. v. Haartman, 1945, 1951, 1956a) it ~~should~~ have been perfectly clear that the female Pied Flycatcher cannot choose in this way, as there is nothing to reveal the marital status of the male. The real-estate threshold is rather a special case than an obligatory conditio sine qua non of polygamy.

The behaviour of the males practising polyterritorial and successive polygamy forms that is known in German philosophy as a Raum-Zeit-Körper (space-time-body), impenetrable to anyone except an ornithologist with plenty of time, coloured rings and a pair of binoculars. For instance, in 1969 a (p.3) I summarized the situation as follows: "In the Pied Flycatcher the different territories of the male may be out of earshot of each other and separated by fields, meadows, territories of other males, etc.; in many cases there will be no contact at all between the females in a triangle and therefore no opportunity for the first female to avoid a mated male". As early as 1945 (p. 30, translated) I summarized the situation in a similar way: "When the female has started to lay, the male disappears from the territory, searching for a new one. He now visits the old territory at most occasionally."

Alatalo et al. (1981) have carefully scrutinized the chances of the female Pied Flycatcher in time to detect the male's marital status, but without finding any support. A similar conclusion was reached by Silverin (1979), mainly from a physiological standpoint. It was to expect that the ecology, ethology, and physiology of the species should point in the same direction, as organisms evolve as an entirety (principle of correlation of functions of Cuvier).

The male's polygamy can best be compared to a matchbox of the Swedish type, with friction surfaces on the two narrow sides, which being opposite to each other, cannot be seen simultaneously. I have heard that an extra-marital relation is known in some South American country as a jonkoping, a mispronunciation of the name Jönköping, printed on the matchboxes, which is the name of the city where most Swedish matches are produced.

The difference of opinion between American and European students of polygamy with respect to the real estate threshold may be as much connected with the sociobiology of the students as with that of their subjects. Europeans grow up reading Mme Bovary, Anna Karenina, and Bel-Ami, Americans looking at the Lone Rider, Davy Crockett, or Tom Dooley in TV. At the American frontier, which still, in spite of the efforts of the eager psychoanalysts in New York and the invention of that perfect secondary territory, the motel, plays such a role in the mentality on the continent, the sex ratio must have been like 100 to 1, and the choice was certainly not that of the man chauvinist.

Prof. Maltsevski (according to a review in Bird Banding) has recently uttered the opinion that polygamy is widespread among birds. Much of this male polygamy may be successive and polyterritorial. Several European species are known to practise this kind of polygamy, even to the extent that the male has ceased to feed his broods (v. Haartman, 1955). In species in which the real estate threshold plays a role, an interesting question will be why the males have not developed the same waterproof way to hide their antecedents as has the male Pied Flycatcher.

Instead of rejecting the unwanted male polygamist, the female Pied Flycatcher meets the threat in two ways. I wish to stress that they may be pre-adaptations and not adaptations ad hoc. The first and more radical method is her short breeding season. The period during which clutches are started may be so short that more than 90 per cent of the females lay within c. ten days (Fig. 11 and v. Haartman 1956b). In e.g. the thrushes and the Dunnock, Prunella modu-

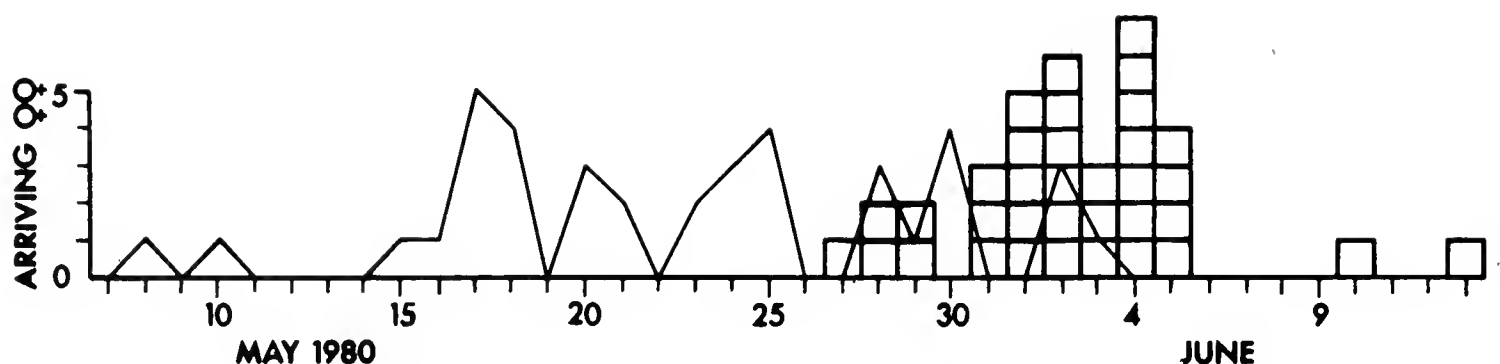


Fig. 11. Commencement of laying in the Pied Flycatcher population at Lemsjöholm in 1980. Squares - dates of starting the clutches; curve - arrival times of the females at the bird station at Lågkär (Åland island, c. 110 km SW of Lemsjöholm)

laris, this time is c. five times longer (v. Haartman, 1969b). Relatively few females are likely to marry at the time when the prospective polygamists pour out into their secondary territories. In my study area the latest clutches of the Pied Flycatcher were laid in the last week of June, whereas males may still be singing vigorously in the first week of July.

The other way in which females meet the threat is by laying reduced late clutches. All or practically all passerines in Northern Europe behave in this way, including faithful monogamists like the tits. In general, it seems likely that the decrease in clutch size is related to a decline in the amount or quality of the food rather than to successive polygamy. In the Pied Flycatcher, however, the decrease in clutch size is unusually large (v. Haartman, 1967a), making it possible that this is an ad hoc adaptation to the increasing frequency of polygyny at the end of the season. The Starling, Sturnus vulgaris, shows a similar, very strong reduction in clutch size, and is also frequently polygamous (Merkel, 1980).

Alatalo et al. (1981) found that the clutches laid by secondary females of polygamous males were smaller than those laid on the same date by the mates of monogamous males. The authors assume that the polygamous male throws off the mask in time to induce her to lay a reduced clutch. This would increase the chances to produce surviving offspring and would form a rudiment of symbiosis in the male's otherwise ruthless struggle to put his genetical stamp upon the generations to follow. I had not time to check this interesting result on my own data.

Although females feeding their brood unaided raise their feeding frequency, they do not attain the level of a co-operating pair, unless the brood is very small (v. Haartman, 1954). Late broods, therefore, have a bad start in life which shows up in the small proportion surviving to maturity (Table 8).

Table 8. Success of young in relation to laying date (data from v. Haartman, 1967a).

| Clutches commenced | Percentage of nestlings mainly recovered in the study area in a later year | Broods fed by female alone |
|--------------------|--|----------------------------|
| May 14-25 | 2.81±0.45 | 2.6% |
| May 26-June 4 | 2.02±0.26 | 8.5% |
| June 5-29 | 1.12±0.55 | 34.5% |

1963

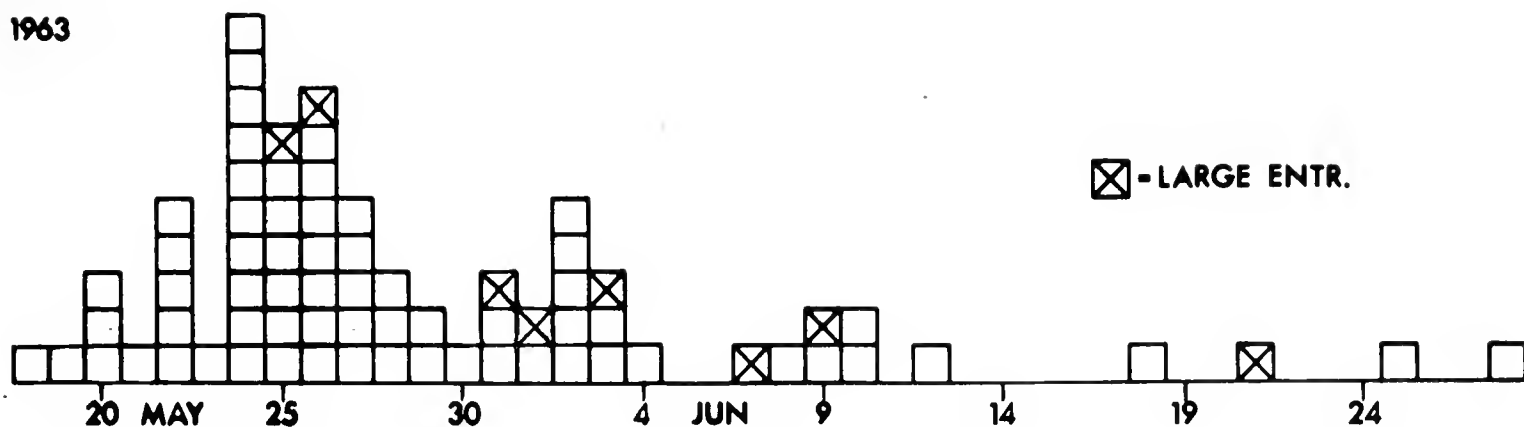


Fig. 12. Commencement of laying in the Pied Flycatcher population at Lemsjöholm in 1963. Squares - dates of starting the clutches. Nest-boxes with an enlarged (diameter = 50 mm) instead of normal (diameter = 30 mm) entrance are marked by cross-hatching

Askenmo (1977) found indications that males feeding too large clutches often died prematurely. Females feeding their young unaided, may well suffer a similar fate. Non-breeding could be preferable to raise a small brood yielding a reduced number of mature offspring. As the mates do not remarry, the death of the female does not lower her mate's "Darwinian fitness", unless her death takes place before their young become independent.

POLYGAMY AND THE FITNESS OF THE MALE

Though bigamous males have a higher number of fledged broods, they will be far from producing twice as many mature young as monogamous males. On the debit side of polygamy we find:

(1) Late females may breed in nest holes of poorer than normal quality (Fig. 12).

(2) Late clutches are small.

(3) Late broods produce few young reaching maturity (paragraph 13).

(4) Polygamous males may fail to feed their first females while these are incubating, and their second females are usually severely neglected. The matrimonial feeding in the Pied Flycatcher may cover the greater part of the energy requirement of the females, and allows her to spend more time incubating (v. Haartman, 1958).

(5) By leaving his first female prematurely, the male runs the risk that neighbouring males obtain stolen matings with her (v. Haartman, 1951a). The effect of this occasional polyandry is very difficult to evaluate.

Again, on the credit side of the polygamous male we should count:

(1) The increased number of broods fledged (1.35 against 0.76 in monogamous males, v. Haartman, 1951, 1969a). To what extent this implies an increase in the number of young surviving to maturity has not been tested. We are still far from a complete understanding of the teleonomy of polygamy.

(2) The first mates of polygamous males lay on an average somewhat earlier than the mates of monogamous males (Table 9). This may be interpreted in two ways. Either early breeding facilitates polygamy, as the males may occupy their secondary territories earlier. Or polygamous males, being on the avera-

T a b l e 9. Median laying date of the mates of five categories of male Pied Flycatchers. The male categories are so arranged that the list **strata** with the lightest and ends with the darkest males. As all x-yr-old polygamous males are likely to be ≥ 2 yrs old, the two last categories should not differ with respect to their colouration.

| | |
|-------------------------------|----------|
| Male monogamous, 1 yr | May 29.5 |
| Male monogamous, x-yr | May 28.5 |
| Male monogamous $\geq x+1$ yr | May 27.5 |
| Male polygamous x yr | May 25.0 |
| Male polygamous $\geq x+1$ yr | May 26.5 |

ge darker, exert a stronger stimulation on their mates. Breeding in the species is fairly independent of the spring **temperature**. Instead, the earlier the flycatchers arrive, the earlier they breed (v. Haartman, 1956b) which led me to the conclusion that the courtship display of the male stimulates the female to produce eggs. Silverin (1975) was able to show that the presence of males had this effect on caged females. It would be worthwhile to study the role of the male's nuptial plumage in this connection.

(3) Whatever the cause of the early laying of the first clutches of plogamous males, they are slightly larger than clutches of monogamous males, because of the connection between clutch size and date (Table 10).

T a b l e 10. Clutch size of the mates of monogamous males and first mates of polygamous males.

| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | N | M | Diff. |
|-----------------|---|---|----|----|-----|-----|----|---|-----|------|-------|
| Monogamous x yr | 2 | 6 | 18 | 57 | 293 | 265 | 38 | 1 | 690 | 6.33 | 0.17 |
| Polygamous x yr | - | - | 1 | 2 | 18 | 26 | 1 | - | 48 | 6.50 | |
| Monogamous | | | | | | | | | | | |
| (x+1) yr | 1 | 3 | 6 | 25 | 143 | 134 | 21 | 1 | 334 | 6.39 | 0.06 |
| Polygamous | | | | | | | | | | | |
| (x+1) yr | 1 | - | - | 4 | 18 | 23 | 1 | - | 47 | 6.45 | |

The difference between the monogamous and polygamous x-yr-old males is 3 per cent, that between the polygamous and monogamous (x+1)-yr-old males is 1 per cent. As a selective factor this cannot be neglected.

ON SEXUAL SELECTION

To summarize, the nuptial plumage of the male Pied Flycatcher has probably evolved, in spite of counter-selection for camouflage, because (a) it seems to give 1-yr-old males a chance to obtain a mate, instead of remaining unmated, and (b) it gives older males a chance of becoming polygamous instead of remaining monogamous. It may (c) perhaps also reduce the (as such small) risks of an old male to remain unmated. The Pied Flycatcher would appear to be an excellent example of what we call "sexual selection".

Now, Darwin was not as happy with his terminology as with his great theory. With an increasing body of facts the Darwinian terms have not seldom received a meaning differing from that in everyday language. When reading about

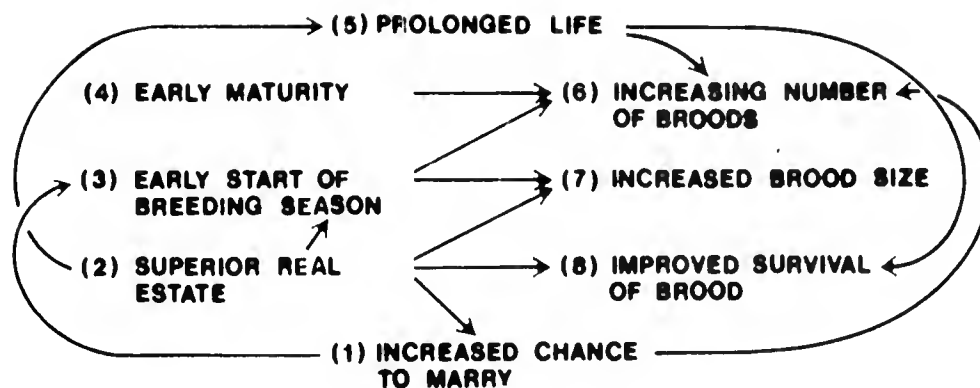


Fig. 13. Threat behaviour of the male Pied Flycatcher. The threatened male is behind the page, somewhat above the photographed male (v.Haartman, 1963)

evolution, one has sometimes the feeling that the language used is that of 1984. Fitness is one of the key words. Ernst Mayr (1971), a worthy follower of Darwin, has called attention to the ambiguity of the term fitness.

Let me give an example. You will excuse me, if I choose one from botany. In my garden I grow several biannual plants, such as Digitalis purpurea, Echium vulgare, and Isatis tinctoria. Then there are the weeds Verbascum Thapsus, and Cirsium lanceolatum. These unrelated plants show a number of convergencies. In the first year they develop a rosette of leaves and a root of considerable size. In the second year, they grow tall to very tall, bloom abundantly and produce either numerous (in Verbascum up to more than 1.000.000, Green, 1981) minute seeds or a few very large ones (Isatis). Then they die. In so doing, they show maximal "Darwinian fitness", not only because they have invested their resources in producing offspring, but also by disappearing from the scene to ensure their offspring a vacant place in which to live. According to my dictionary a synonym of fit is lively, but this would be too much to say of a dying Digitalis.

The term fitness does not cause any difficulty to professional biologists, but to the public at large it certainly does. Today, nearly 125 years after the great theory was published, it is still ignored, misunderstood, or contradicted, not only among extreme fundamentalists, but among liberally minded and educated people, too.

Scientists carry a great deal of responsibility for this. Darwinism, in its modernized version, is a corner-stone of the knowledge of mankind, and scientists are responsible for its presentation not only as correctly, but also as logically and understandably as possible.

Darwin left us with three modes of selection: natural, artificial, and sexual selection. This is a division on two levels. Natural and artificial selections are opposites, but sexual selection is not related in this way to the two others. All, or practically all, selection is through differential reproduction, and in higher animals this is usually sexual.

Darwin (1859, 1871) introduced sexual selection to explain as I would express it, why living beings in certain cases cede from fitness in the original sense of the word, in order to produce more numerous offspring, that is, to obtain "Darwinian fitness". What we really ought to stress today is the similarity between natural and "sexual" selection. Figure 13 gives a simplified picture of factors, promoting reproductive success in male Pied Flycat-

chers, but it may with slight changes be applied to numerous other birds. The role of possible counter-selection was not estimated.

Take, for instance, a successful struggle for life, resulting in a prolonged life-span, i.e. fitness in the original sense of the word. Prolonged life has no selective value, or rather negative selective value, unless it (a) allows the individual to reproduce at least once more, (b) allows the individual to live until its brood has become independent. Though mortality is increased during the breeding time (v. Haartman, 1951b, 1971), the risk of dying during the time needed for the young to become independent must be much smaller than the risk of dying before the next breeding season, the former risk being, in addition, alleviated by the chance that the mate will stay alive and may save part of the offspring from starving to death. The main premium of a successful struggle for life is, thus, one or more extra broods, i.e. what is thought to be the quintessence of sexual selection.

Naturally, one could divide selection according to the main object involved, e.g. into sexual, foraging, anti-predator, migratory, etc. selection, but the only result of this would be to obscure the mechanism through which all selection works. We could go on, analyzing Fig. 12 point after point, and find similarities between the presupposed sexual selection and the natural selection. Their functional difference is too small to uphold them as different "subspecies" of selection.

It has been maintained that in sexual selection the female always makes a choice between alternatives. This is not necessarily the case. Let us assume that the female Pied Flycatcher mates with the first male with a nest hole that she meets. One female happens to mate with a male with bright colouration, another female mates, under otherwise identical conditions, with a female-like male. The display of the more colourful male stimulates his mate so that she starts to lay somewhat earlier than the mate of the female-like male. The known facts do not contradict this assumption (see Table 9). The darker the group of males in the table, the earlier the females laid, and consequently, the larger were their clutches (see Table 10).

We may assume that the Pied Flycatcher had an ancestor showing nest-demonstration (paragraph 6) before he had evolved the colouration enhancing this behaviour. The movement is older than the enhancing structures, as Lorenz stated already in the thirties (e.g. 1935). The male Spotted Flycatcher, Muscicapa striata, lacks dramatic colours, except for the yellow mouth cavity, visible when he sings, but has a nest-site demonstration, with which he courts the female (v. Haartman et al., 1963-72). In this respect the courtship of the Spotted Flycatcher is more primitive than that of the Pied Flycatcher, but it is more advanced in that it is used also on sites not suitable for nest building; it has to a certain extent freed itself from its original context.

Soon after the process suggested above has started, the evolution is likely to change character, provided there is not enough selection pressure to counteract it. In the female there will be a premium upon choosing bright males, in males, a premium upon being brightly coloured.

This is, however, no mechanism restricted to "sexual" selection as opposed to other situations in which releasers or signals evolve. In his classi-

cal text-book, Tinbergen (1951), quoting the speculations of Haldane and Huxley on hyperthely, suggests that the use of the sumptuous canines of sabre-toothed tigers as signals in encounters with other individuals of the species caused these teeth to evolve to an extent that marred their original function. Although recent palaeozoology has shown that these teeth were actually in harmony with the feeding ecology of the animals it is likely that structures may in fact evolve that facilitate social co-operation but, at the same time, endanger their carrier. The nuptial plumage would be an example, but nuptial plumage is only one special case. There are also structures used to threaten other males in territorial fights or fights for social rank, or signals to serve the parent-off-spring relations, or signals to keep the flock united in gregarious species. That these social releasers may be dangerous to their owners is shown by the different ways in which they are hidden when not in use. If we really want to have a special category of selection it ought to be social instead of sexual selection.

THE STONE THAT ROLLS UPHILL

There is a slight but interesting chance that social selection will, at least momentarily, favour the evolution of genotypes contributing less than normal to the gene-pool of coming generations. This chance is connected with the way social information is transmitted in animals with a certain level of organization. An individual, the actor, gives a signal (movement, usually enhanced with special optic, acoustic, olfactory, etc. stimuli). In another individual, the reactor, this releases a response thanks to an innate releasing mechanism (IRM), which is like a lock designed to receive the key stimuli presented by the actor.

Almost all comprehensive studies of innate releasing mechanisms have revealed that they share a number of common characteristics. (1) In contrast to learned responses, they are not "searching images", but a response to very simple key stimuli. It is as if the reactor would possess a description (English lacks the better word *signalement*, used in many other languages) instead of an image of the object of its reaction. (2) The optimal key stimuli are not those offered by the normal object of the reaction, but rather exaggerations thereof. (3) IRMs may be very conservative.

For a Ringed Plover, Charadrius hiaticula, or an Oystercatcher, Haematopus ostralegus, the optimal stimulus to rolling an egg back into the nest is not given by their own egg but by a much larger one, as is easily seen if both are offered simultaneously. The optimal mate of the male of the butterfly Argynnis paphia would use swifter wing strokes than those of the species (Magnus, 1956). The male of another butterfly, Satyrus semele, would prefer a mate darker than the S.semele female (Tinbergen et al., 1943). Many human males would prefer Marilyn Monroe to any girl they are likely to meet in reality.

In some cases the key stimuli may be signs of ability to reproduce successfully, as pointed out by Lorenz (1943). The paradoxical selection for the nuptial plumage as a handicap (Zahavi, 1975, 1977) would have the same function. Those males surviving in spite of the handicap would, so to say, carry a certificate of being superior to their competitors in other respects. The

IRMs responding to such key stimuli would, then, have strong reproductive value.

In other cases, again, it seems possible that the "supernormal" objects of the IRMs in no way show improved reproductive output, but rather the contrary. This would be the case if their alternatives, which failed to mate, were potentially able to have more offspring surviving to maturity. This situation can most easily be imagined with respect to the female's choice of mate, but signals belonging to other Funktionskreise could indirectly have the same effect, e.g. signals used in territorial encounters.

Why IRMs favour supernormal stimuli we do not know. It may well be that mechanisms which worked more exactly would be too costly, and that the IRMs are, generally, the best possible construction even though, in special cases, they cause evolution of types with reduced reproduction - an apparent biological counterpart to a stone rolling uphill.

The conservatism of the IRMs may cause them to be relatively resistant to natural selection. There is the famous case of the female Three-spined Stickleback, Gasterosteus aculeatus, on the Olympic Peninsula, where strong predation has caused a change of the male's red nuptial colour to black, but where the majority of females still, after thousands of years, prefer the originally coloured males (McPhail, 1969; see also May, 1971).

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CONTRIBUTION OF RUSSIAN AND SOVIET ORNITHOLOGISTS
TO PALEARCTIC ZOOGEOGRAPHY

Eerik Kumari

Institute of Zoology and Botany of the Estonian SSR Academy of Sciences,
21 Vanemuise Street, 202400 Tartu, USSR

For long years one of the most outstanding figures among contemporary Soviet ornithologists was Georgi Petrovich Dementiev (1898-1969), who thanks to his wide range of interests, great erudition, unusual capacity for work and keen response to the needs of science soon rose to the leading position in soviet ornithology. This distinguished place he continued to occupy all through the postwar years.

The vast expanses of the territory of the Soviet Union, its diverse natural conditions and rich fauna obviously played an important role in the development of Dementiev's scientific interests. Besides other branches of ornithology he was particularly interested in the distribution of birds and already in 1937 he published a long article on this problem - "An analysis of the main elements of the avifauna of the Eastern Palearctic". Questions of zoogeography on which he later wrote, a number of other interesting articles, preoccupied the scientist up to the end of his days.

We propose to give a survey of the contributions of Russian and Soviet ornithologists to the study of Palearctic zoogeography as this subject is closely connected with the interests and achievements of the late eminent Soviet ornithologist.

We shall discuss the following points:

1. The contribution made to the development of Palearctic ornithogeography by the investigations of P.S.Pallas and the scientific expeditions organized by the St. Petersburg Academy of Sciences in the 18th century.
2. The golden age of faunogenetical (historical) zoogeography.
3. New ornithofaunistic investigations.
4. Natural zonation and faunal complexes.
5. Faunal type as a new concept in zoogeography.
6. The question of zoogeographical boundaries and faunal regions.
7. The zoogeographical aspects of bird migration.
8. Some special problems of regional zoogeography.
9. The Progress of ecological studies.
10. Efflorescence of ecological zoogeography.
11. At the sources of synthetical ornithogeography.

THE CONTRIBUTION MADE TO THE DEVELOPMENT OF PALEARCTIC
ORNITHOGEOGRAPHY BY THE INVESTIGATIONS OF P.S. PALAS AND
THE SCIENTIFIC EXPEDITIONS ORGANIZED BY THE St.PETERSBURG
ACADEMY OF SCIENCES IN THE 18th CENTURY

The classics of the biological sciences of the first half of the 18th century Linné, Brisson and Buffon had laid a basis for the classification of animals. Their material, however, was insufficient to draw any weighty zoo-

geographical conclusions. It was precisely at that time that the great powers England, France and Russia started dispatching to various parts of the world large expeditions including also naturalists of different specialities. Collection of zoogeographical materials began.

In 1725 the Russian Academy of Sciences was founded and one of its most important tasks was the study of the natural resources of the country. From the very beginning its activities included preparing and sending large expeditions to different parts of the immense empire. In 1732 a large expedition set out for Siberia under the leadership of S.P.Krasheninnikov, I.G.Gmelin (Sen.) and other naturalists from the Academy of Sciences. In the course of almost ten years Krasheninnikov succeeded in gathering a great wealth of material about the natural conditions in East Siberia, especially Kamchatka, among which zoogeographical generalizations occupy an important place.

Already the very first expeditions like all the later ones organized by the Academy of Sciences to the eastern and southern regions of the Russian Empire engaged in investigation into birds, their distribution and way of life, which provided much new scientific information that had been unknown before. Birds became models on the example of whose distribution different kinds of zoogeographical conceptions were developed.

In the second half of the 18th century the Academy continued sending expeditions to different parts of Russia and the adjoining territories. Academician I.I.Lepiokhin spent four years studying the nature of Eastern Europe and Western Siberia together with his collaborators. His findings made him put forth an idea of the existence of natural zones and the influence of climate on animals. During the same time S.G.Gmelin (Jun.) travelled about Southern Russia, where he discovered a number of new species of animals to which he gave Latin names. Academician I.I.Georgi, whose exploration journeys took him to South-Eastern Russia and Siberia, succeeded in establishing 222 forms of birds in these regions.

But the greatest Russian ornithologist of the 18th century was Academician Peter Simon Pallas (1741-1811), an energetic organizer, member of several scientific expeditions organized by the Academy, and curator responsible for the publication of their results. Born in Berlin, he entered the service of the Russian Academy of Sciences in 1767. The results of a large expedition exploring the eastern regions of the European part of Russia and Siberia from 1768 to 1774 were published in a three-volume monograph (1771, 1773, 1776), which gives detailed descriptions of the natural conditions and animal realm (including birds) of the localities investigated. From 1786 to 1794 Pallas performed the duties of scientific leader of an expedition to the Far East, in which he, however, did not personally participate. In 1793-1794 he undertook a scientific exploratory journey to the southern provinces of Russia.

All the above-mentioned expeditions carried out by Pallas, his collaborators and contemporaries provided for the Zoological Museum of the Academy of Sciences in St.Petersburg a big collection of different materials among which birds occupied a prominent place. On the basis of these materials Pallas published his famous two-volume monograph "Zoographia Rosso-Asiatica", in which 271+374 pages were devoted to birds (425 species).

According to G.P.Dementiev (1940) the beginning of ornithological research in Russia should be regarded as going back to the 18th century. The expeditions organized by the St. Petersburg Academy of Sciences were the most comprehensive ones undertaken in those days and yielded the best results. A considerable proportion of their scientific results concern birds. Besides the works of Pallas the results of these expeditions have been discussed in the publications of several other participants. Pallas himself described over 20 new species of Palearctic birds.

THE GOLDEN AGE OF FAUNOGENETICAL (HISTORICAL) ZOOGEOGRAPHY

In the 19th century a large number of important works were written on the birds inhabiting different regions of Russia. Monographs were published as separate books or as volumes of several series of the Academy of Sciences. The Moscow Naturalists' Society began to issue its own bulletin and the Russian Geographical Society its transactions later entitled "Articles on the Russian Empire and the Bordering Asian Countries" and Materials on the Fauna and Flora of the Russian Empire. All of these offered space for the publication of long faunistic overviews.

Thus, a number of surveys appeared of the birds inhabiting different parts of the country: the Orenburg Territory by E.A.Eversman, the Kiev school district by K.F.Kessler, the Voronezh Government by N.A.Severtzov, the Volga lands by M.N.Bogdanov, and a treatise on Siberian fauna by A.Th.Middendorff. All of these contained abundant factual material about the distribution and biology of the birds found on the territory of the Russian Empire and laid a basis for the later ornithogeographical studies. The authors of these publications were research workers of the Academy of Sciences, professors of universities and other men with a higher scientific qualification.

From the middle of the 19th century, after a considerable amount of ornithofaunistic material had been gathered from various places, mostly from the European part of Russia, Turkestan and Siberia, historical (now called faunogenetical) zoogeography began to develop and it was to remain the prevailing trend in Russia for long decades to come. It started with the classical zoogeographical works of three eminent Russian specialists in this field - N.A.Severtzov (1827-1885), M.A.Menzbier (1855-1935) and P.P.Sushkin (1868-1928). At the beginning of their activities the two former stressed the primary importance of the ecological factors in the distribution of animals, but later they became classics of the historical trend. Now a golden age began in historical zoogeography, which took great interest in the genesis of fauna and in the factors influencing its origin and evolution.

The scientific thesis of N.A.Severtzov (1855) dealing with the periodically occurring phenomena in the lives of the terrestrial vertebrates in Voronezh Government is built up on a firm ecological basis and, therefore, this work should be regarded as one of the first ecological monographs written in Russia. Of course, the word "ecology" was not yet used in the scientific terminology of that time, but the contents of the thesis show that this is precisely what the author meant. In another monograph (1873) about the vertical and horizontal distribution of animals in Turkestan N.A.Severtzov summarised the results of his long years of research conducted in Central Asia. It is interesting to note that in this work he discusses the contemporary distri-

bution of animals taking into account not only their existing, but also their historical living conditions.

The extremely scanty paleogeographic information available for the region under consideration in those days did not allow Severtzov to put forth any firmly grounded hypothesis of a historico-zoogeographical nature, recent investigations, however, have proved the correctness of many of his conclusions. He was the first to put forward the assumption that comparative analysis of the present distribution of animals would enable us to elucidate the nature of the living conditions in the geological past.

N.A. Severtzov was the first in Russia to draw up zoo(ornitho)geographical divisions of the Palearctic region (1877), on the basis of a critical analysis of the subdivisions of this region suggested by the English scientist Wallace. Severtzov bases his zoogeographical divisions on the peculiarities of the landscape taking into consideration the natural zonation of our continent. Apart from the historical conditions he takes into account also the contemporary physical and geographical conditions of the distribution of birds.

The second half of the 19th century also saw the appearance of the fundamental works of the greatest Russian ornithologist and zoogeographer M.A. Menzbier, whose two-volume monograph "The Birds of Russia," 1895 provided the first comprehensive survey of the ornithofauna of the European part of Russia and the Caucasus. With this significant work Menzbier became the founder of Russian ornithology. In his scientific thesis dealing with the ornithological geography of the European part of Russia (1882) he proposes zoogeographical divisions of the territory based on six natural zones: the tundra, the taiga, the forest steppe, the steppe, the littoral and the islands, the desert. He emphasises that the division of local avifaunas should be based on the information gleaned from the study of the contemporary natural conditions and the distribution of separate species and not on higher taxonomic categories.

The scientific heritage of the founder of Russian ornithology is very rich and varied. There is no time to discuss all his works. We shall mention here only the most important ones, which include a book in three volumes on game birds, a large popular-scientific book on the birds of the world, a zoogeographical atlas, a book on the zoological divisions of the Turkestan Territory, an article on the origin of the tundra fauna, etc. Of great interest is his survey of the history of the fauna of the European part of the USSR (1934a), which appeared a year before his death. In this work Menzbier shows himself as an ardent defender of faunogenetical zoogeography - a trend which became more and more pronounced in the works he wrote during the last decades of his life.

Perhaps Menzbier as a zoogeographer has been best characterized by I.I. Puzanov (1946). He writes that many of the truths of the initial period of Menzbier's activities were proved erroneous in later years. In his old age Menzbier was of the opinion that the phenomena of the biosphere and those of the lithosphere should only be studied hand in hand. "Contrasting this laconic and wise opinion with the isolent disdain expressed by the young Menzbier for problems of historical zoogeography one cannot help but feel that the taste for history comes with years..." (Puzanov, 1946, p. 26).

If N.A. Severtzov and M.A. Menzbier may be regarded as two like-minded scholars the views of the same scientific school in Moscow, then the third member

of the triumvirate - P.P.Sushkin (1868-1928) - worked for many years at the Institute of Zoology of the Academy of Sciences of the USSR in Leningrad.

During the first decades of his scientific activities P.P.Sushkin wrote a number of long avifaunistic surveys covering different regions of the country (Ufa Government, the Minusinsk Territory, the Central Kirghiz steppe, etc.), which were brought to completion with a posthumous publication, a two-volume book entitled "Birds of Soviet Altai", 1938. His scientific testament is a work on the zoological regions of Central Siberia and the nearest parts of the Asian Highland and the history of the contemporary fauna of Palearctic Asia (1925), which attracted much attention both at home and abroad.

Sushkin claims the existence of two faunal complexes of birds in Palearctic Asia: one of Asiatic character east of the river Yenisei, and another of West Palearctic character west of this river. The differences in their composition cannot be explained only with the influence of the contemporary ecological factors. Historical reasons clearly play a part here. The fauna of the territory beyond the Yenisei is much more ancient than that of Western Siberia, containing a number of Central-Asian elements. Many of the transpalearctic Asian species have immigrated to this region comparatively lately. Using the data on the distribution of the birds (and other animals) Sushkin explains the development of the climate, landscape and living nature of Asia in the past. The fauna of Siberia and that of North America have many similar features, which corroborates the idea of a mutual exchange of faunal elements between these two continents in the past. It is possible that there once existed a certain continent-Beringia-between them.

Sushkin's theoretical speculations in this particular work as well as in his other writings are extremely interesting. They enable us to follow step by step the evolution of faunogenetical zoogeography in Russia. The ideas of Severtzov, Menzbier and Sushkin have exercised a fruitful influence on the development of the work of other Russian and Soviet zoogeographers up to the present time.

According to Dementiev (1958) the geographical distribution of birds provides ideal material for zoogeographical generalizations. A drawback here is the scarcity of the paleontological material available on birds. In zoogeographical analysis greatest attention should be paid to breeding birds. But the migration of birds and the spread of the different species should also be taken into account.

E.V.Kozlova (1952, 1975), Sushkin's disciple and later collaborator, continued the faunogenetical investigations into the Tibetan Highland and the zonal steppes and deserts of Central Asia. This fauna is very peculiar, but rather poor in species. The desert zone of Central Asia is somewhat more ancient than her zone of steppes. The avifauna of Central Asia shows close links with the faunas of the steppes, savannahs and deserts of palearctic and tropical Africa, its links with the steppe birds of Eurasia are considerable weaker, and they are still weaker as regards the forest avifauna of China and the birds of the forest steppes of India. The representatives of the avifauna of Central Asia have ancient mutual links with the faunas of other countries. In all probability the African open landscapes and their avifauna are more ancient than the steppes and deserts of Central Asia and

their inhabitants. The prevailing direction of the spread of birds has been from the west to the east.

In a work dealing with the arctoalpine avifauna and its origin A.A.Kishchinsky (1974) puts forward arguments for the restoration of fauna by the biogeographical method. According to him the characteristic species of migratory arctoalpine birds primarily formed not in the mountains, but far from the arctic or alpine landscapes. The genetic roots of the arctoalpine avifauna lie in Eurasia (in the north of Eastern Siberia) from where some species later immigrated to North America through the Bering region.

A.A.Kishchinsky (1977) is also of the opinion that in order to get more reliable information it is indispensable to combine the paleontological and biogeographical methods. In the future, too, the study of the history of fauna will remain a topical problem of zoogeography. The genetic diversity of each fauna makes it necessary to investigate the history of its separate species as well as the evolution of its ecosystems. The author, who is a convinced supporter of faunogenetical zoogeography, puts forward a number of progressive principles for future research including the use of paleontological and paleogeographical data in the study of the contemporary distribution of birds, thorough investigation into the ecology of birds, their spreading, trophic links, etc. The study of the shifts in the boundaries of the distribution areas and the changes in the distribution of the separate bird species within the ranges is one of the most interesting tasks facing zoogeography.

The faunogenetical trend in zoogeography is by no means a past stage in ornithological research in the USSR. New investigators equipped with modern, improved knowledge of the principles and ways of the development of fauna, with new methods of investigation and more sophisticated devices for field and laboratory work are continuing the work started by the classics of Russian zoogeography.

NEW ORNITHOFAUNISTIC INVESTIGATIONS

After the Great October Socialist Revolution conditions were created for extensive ornithological investigation in all regions of the country and several new research centres were set up. This resulted in brisker publishing activities and a number of ornithological works were printed in the course of the following years. Especially great progress in this field has been made in the period following the Great Patriotic War.

Besides the appearance of the important ornithofaunistic surveys of the last decades of the past century, the first decades of the present century made substantial additions to the materials dealing with the bird fauna of the European part of the USSR and other geographical regions of the country including Siberia and Central Asia.

An especially important event in the study of the avifauna of the USSR was the appearance of the issues of a new series entitled "Fauna of the USSR". A similar series had been published also before the Revolution, separate volumes of which were devoted to birds. Now the first volume dealing with birds was printed in 1937. In the course of the last 45 years separate volumes have been published about diurnal raptors (Stegman, 1937), the ornithogeographical divisions of the Palearctic region (Stegman, 1938), the waterfowl (Tugarinov, 1941), divers and grebes, petrels and shearwaters, cormorants, storks and

flamingos (1947), auks (1957), waders (Kozlova, 1961, 1962; Yudin, 1965). From 1951 to 1954 was issued a fundamental survey "Birds of the Soviet Union" edited by G.P.Dementiev and N.A.Gladkov, which completed the recent stage in the study of the birds of the Soviet Union.

Besides the above-mentioned surveys many of the separate Union republics or large geographical regions have also published their own "avifaunas" in the post-war years. The bulkiest of these is the five-volume "The Birds of Kazakhstan," 1960-1974 edited by I.A.Dolgushin and his disciples. The other Central Asian republics, too, have their own avifaunas - Uzbekistan (3 volumes, 1953-1961), Kirghizia (3 volumes, 1959-1961), Tadzhikistan (3 volumes, 1971-1977), Turkmenistan (Dementiev, 1952; Rustamow, 1958). On the Ukraine three volumes have appeared to date (1957-1979) and two volumes dealing with the western regions of the Ukrainian SSR (1963), Moldavia has published two volumes (1970-1971) and Byelorussia one volume (1967). The birds of Lithuania are described in a three - volume book (Ivanauskas, 1957-1964) and the birds of Estonia in a book by E.Kumari (1954).

In addition to the works mentioned above a large number of books or long articles in various journals have been published about the bird fauna of different parts of the USSR.

NATURAL ZONATION AND FAUNAL COMPLEXES

A characteristic feature of Russian physical geography and also biogeography is the division of the immense territory of our country into natural (landscape or geographical) zones. These zones run meridionally and each possesses its own physico-geographical as well as biological (ecological) peculiarities. The investigations of two classics of Russian geography, V.V.Dokuchayev and L.S.Berg, contributed greatly towards the division of our territory into natural zones. Their example was followed by biologists, ornithologists included. In the works of the classics of Russian ornithogeography we can already find cases where the territory under discussion is divided into natural zones.

The principal Palearctic natural zones from the north to the south are the following: the tundra, the forest zone (the taiga), the forest steppe, the semidesert, the desert. The Soviet biogeographer Yu. I. Chernov (1975) gives a more detailed division of these zones into subzones and azonal units. In addition to these he also distinguishes intrazonal units, which have played an essential role in the genesis of the flora and fauna. The zoogeographical divisions do not necessarily coincide with the divisions of general geography.

In their early works N.A.Severtzov (1877) and M.A.Menzbier (1882) introduced the arrangement of vast territories into zoogeographical regions on the principle of natural zonation, which they called landscape (natural) complexes. This tradition is still followed in the works of later Soviet zoogeographers and ornithogeographers.

Thus, for example, G.P.Dementiev (1937) based his analysis of the main avifaunal elements of the Eastern Palearctic on separate faunal complexes, meaning by this term similar faunal groupings within the limits of definite zones resulting from historical development. However, he does not give any exact definition of the meaning of this term, which most probably is a

synonym for the term "faunal type" used by B.K. Stegman, who in the 1930s elaborated his own scheme for the ornithogeographical division of the Palearctic region.

In the above-mentioned survey Dementiev distinguishes in the ornithofauna of the USSR the following faunal complexes corresponding to the basic landscape or geographical zones of the Palearctic region: arctic fauna, boreal or taiga fauna, transitional fauna (the zones of deciduous forests, cultivated landscapes and steppes), mediterranean fauna, Asian highland fauna, and Manchurian or Japanese-Chinese fauna. As we see, here the author does not make a clear distinction between the concepts "faunal complex" and "fauna".

Twenty years later G.P. Dementiev (1958) returned to the problem of dividing the Palearctic region into natural zones and suggested the following scheme for distinguishing the avifaunal complexes on the territory of the USSR: 1. The Arctic zone: (a) the littoral subzone, (b) the tundra subzone, (c) the forest tundra subzone. 2. The forest zone: (a) the taiga subzone, (b) the subzone of mixed and deciduous forests, (c) the subzone of forest steppes. 3. The zone of open dry landscapes: (a) the steppe subzone, (b) the subzone of semi-deserts and deserts. 4. Mountains (a zone or an intrazonal group of landscapes): (a) the subzone of boreoalpin highlands, (b) the mountain forest subzone, (c) the subzone of mountain steppes and deserts.

In the author's opinion the above division fully reflects the history of the avifauna. The distribution of birds on the territory of the USSR is strictly zonal corresponding to definite complexes of physico-geographical, and consequently also faunistic conditions. The evolution of the avifauna proceeded in complete accordance with the formation, development and alteration of the basic natural zones.

Investigating the fauna of vast territories in terms of their natural zonation it is necessary first to give a more exact definition of the concept "faunal complex", to establish whether "faunal complex" and "faunal type" are complete synonyms or two separate concepts almost similar in meaning, which different authors use to designate different notions. According to the definition offered by A.K. Rustamov (1963) a "faunal complex" is a group of species closely linked by common origin, development and existence in a definite ecologo-geographical environment. At the same time a "faunal type", according to the same author, is much narrower in meaning and can only be used in reference to a small part of a whole faunal complex.

N.V. Tupikova (1975) has suggested the following definition of the concept "faunal complex": a specific set of species with similar distribution, linked with definite types of landscapes by their common development; as a result of their common evolution the species have become adapted to each other and to the natural territorial complexes characteristic of the given landscape type, here they find optimum conditions for existence (attain their greatest numbers) and dominate among the animal population; each faunal complex is represented by a specific spectrum of living forms.

Many Soviet zoogeographers are of the opinion that faunal complexes should serve as a basis in establishing the boundaries of faunal regions and, likewise, they should be taken into account in determining the interrelations of the faunas of large territorial units.

In the 1930s a large number of articles in different journals and a special monograph were published by B.K. Stegman (1938), a disciple and close collaborator of P.P. Sushkin, about the principles of the ornithogeographical division of the Palearctic region. In these articles he put forward a number of original ideas regarding the methods of investigation into faunal complexes (faunal types) and the compilation of zoogeographical maps. He maintained that the method so far used for the division of territories into zoogeographical regions by means of linear boundaries is purely formal. He proposed a method based on the study of separate faunal types with similar origin spread, which besides giving a picture of the faunal dynamic, unites zoogeography with ecology: the ornithofaunal types of the Palearctic region are in significant correspondence with its landscape zones.

His method of compiling zoogeographical maps on which the distribution of the faunal types is shown by means of spots of different colours is essentially new and excited great interest among Soviet as well foreign zoogeographers. At the same time, the concept "faunal type" does not meet with universal approval by zoogeographers and actually it means very much the same as the "faunal complex" of other authors.

Stegman himself (1938, p. 6) defined the concept "faunal type" with a view to the zoogeographical subregions of the Palearctic as follows: "...taking into account the principle of uniting the faunal groupings according to their origin and also the possibility of the mutual penetration of the different elements on large territories, I consider it more appropriate to replace the purely geographical term "subregion" by the term "faunal type". In this case besides the Arctic (which constitutes an independent region), we shall have the following six types of Palearctic fauna: 1. Siberian, 2. European, 3. Mediterranean, 4. Mongolian, 5. Tibetan, 6. Chinese ... The number of the bird species serving as the basis for the following description of the faunal types is very large, running into nearly 900."

As we see from the above, the "faunal type" is nothing else but the "old" faunal complex projected against the background of the geographical subdivisions (subregions) of the Palearctic. In establishing the faunal types the natural zonation as well as the geographical distribution, history and contemporary ecology of the fauna are taken into consideration.

Stegman's zoogeographical principles constitute a step forward in the further development of the theory and views of the classics of Russian zoogeography.

B.K. Stegman's prolific activities in developing Soviet zoogeography are proved by the large number of articles he wrote in the 1930s. These became widely known and were often referred to by European zoogeographers. In the post-war years, however, he devoted much less time to the study of this field. Thus, in an article on the regularities governing the distribution of the avifauna of the taiga (1966) he merely repeats his earlier views on the composition of the Siberian faunal type, maintaining that most of its species inhabit the eastern region, whereas in the west they mainly live in spruce forests. The bird faunas of Siberian and North American coniferous forests are of common origin, having had contacts in the past in the region of the

hypothetical Beringian continent. As to the avifauna of the Eurasian steppes (Stegman, 1955), it was chiefly formed as late as the Quaternary Period and is comparatively poor in species. The fauna of deserts is more ancient than that of steppes.

The concept of faunal types has been approved by several contemporary faunists and zoogeographers (Chozatskij, 1975). In the polar region of the Ural Mountains and on the Yamal peninsula the interrelationship of the tundra and forest elements of the ornithofauna is easy to trace in the local ecosystems. On the strength of recent investigations V.V. Brunov (1980) has concluded that in the Eurasian taiga there is no single centre of speciation, and that the faunal complex (faunal type, faunula, faunal grouping) of the taiga has centres of origin in several regions. On the basis of the similarity of the optimum sites in the breeding areas he distinguishes ten large faunal groupings in the ornithofauna of the Eurasian taiga. There are five faunal groupings whose optimum sites are either only in the taiga or both in the taiga and some other zones and belts. Such birds have the optimum sites of their ranges in: 1. the northern, central, and partly southern larch taiga; 2. the southern fir taiga; 3. the southern fir taiga and non-taiga forests; 4. the subalpine belt of the mountains in North-Eastern Eurasia and Southern Siberia; 5. forest tundra and southern tundra.

As for the interrelationship of the European and Chinese faunal types, besides asserting their basic differences E.N. Matyushkin (1975) also points out some features **which** they have in common. The characteristic peculiarities include secondary sympatry of the western and eastern forms, the Upper-Pliocene base of the fauna of broad-leaved and coniferous broad-leaved forests as well as of the forest steppes of the Palearctic region, etc. The composition and genetic interrelations of the bird species of the Mediterranean faunal type have been analysed by I.A. Dolgushin (1958), who maintains that the Mediterranean fauna is a special zoogeographical unit, which has developed under impact of specific natural conditions and according to the historical formation of the main landscape types.

THE QUESTION OF ZOOGEOGRAPHICAL BOUNDARIES AND FAUNAL REGIONS

According to S.S. Schwarz (1975) the interrelation of the boundaries of separate species and whole biological complexes can be caused by two circumstances: either the natural conditions a) make impossible the existence of a species or a complex of species beyond the limits of a certain zone, or b) allow the existence of a certain species, but reduce its biotic potential. The geographical distribution boundaries of living beings are comparatively stable, however, they can change under the influence of alterations in living conditions. L.A. Portenko (1965, 1974) has pointed out that detailed mapping of the distribution boundaries of a number of palearctic bird species refer to the possibility that during the last hundred years the boundaries of the ranges of many species may have changed considerably.

Over recent years much material has accumulated in Soviet ornithological literature on the changes taking place in the boundaries of the ranges of a large number of bird species as a result of both natural (climatic and biotopic) and human factors in the Baltic region (Kumari, 1958a, 1958b) in the

Ukraine (Strautman, 1960), in Siberia (Syroetchkovskii, 1960), in Central Asia (Schnitnikov, 1948) and in other regions. From the zoogeographical point of view it is important to investigate the boundaries of the distribution areas and the changes taking place in them with regard to separate species and still more as concerns whole faunal complexes and the spatial categories of their habitats.

The representatives of classical faunogenetic zoogeography (Portenko, 1965) had based their zonation of territories on the distribution of animals (often relict or endemic species) without taking into account the landscape zones which had been the base of the latter. In the opinion of Yu. I. Chernov (1975) the types of animal communities and not faunal complexes should correspond to zonal subdivisions. The zonal communities of birds do not coincide with the faunal divisions. This principle was already observed by N. A. Severtzov (1877) and is followed by many Soviet zoogeographers nowadays.

Thirty years ago B. A. Kuznetsov (1950) published a book "Zoogeographical Division of the USSR into Regions," in which on the basis of mammalogical materials he pointed out the shortcomings of the division of territories into separate regions used by classical zoogeography. He proposed a new scheme based on the zonal principle. Since that time numerous papers have appeared (Rustamov, 1958; Strautman and Tatarinov, 1958; Uspenskii, 1960; Kuzyakin, 1975, and others) in which landscape zones are used as zoogeographical subdivisions. In Soviet zoogeography a number of new terms have been coined, e.g. "background species", "landscape animals", "landscape zoogeography", etc. In A. P. Kuzyakin's opinion "zoogeographical divisions can only be set up on all embracing basis, on that of landscape zones. The isolation of "faunal regions" is contradictory to scientific thinking. And the branch (zoological) division into faunal complexes should be called faunistic division (p. 132). Such statements may seem somewhat strange to many biogeographers, nevertheless they are not devoid of a rational kernel.

The last to divide the territory of the Soviet Union into ornithogeographical regions on the principles of classical zoogeography was L. A. Portenko (1965). According to him the division of territories into regions should serve the aim of determining the objective distribution of the faunal complexes belonging to different grades found on certain territories. The division of territories **into** ornithogeographical regions is first and foremost built up on the exactly established ranges of the birds inhabiting them. Therefore, areological investigations are of primary importance in zoogeography.

As is known, M. A. Menzbier (1882) in his "Ornithological geography" developed an approach to zoogeographical division into regions on the basis of landscape zones, which he abandoned in his latest works. Criticising the Menzbier-Sushkin **schema**, V. V. Kucheruk (1972) does not recognize the regional-faunistic divisions as a basis for zoogeographical division of territories into regions, he accepts only the zonal-landscape principle. In his opinion zoogeographical boundaries are always also ecological, i.e. determined by the landscape.

An intermediate position regarding the attitude to the principles of dividing territories into regions proposed by the classics of Russian historical zoogeography is held by J. I. Chernov (1975): "The authors who are trying

to reduce the division of territories into zoogeographical regions to one based on landscape zones usually prove their point by referring to the great similarity of the animal kingdom within the limits of a geographical landscape zone. They do not take into consideration the fact that none of the widespread species came into being in the zone in general, but in a definite part of it, most often long before the formation of the present boundaries of the zone, and that each must be connected with a certain faunal centre. Therefore, contrasting whole faunas, which are more representative in the faunogenetical respect, is no less formal than dealing with endemic and relict species only...."

A.G.Voronov (1975) discusses the interrelations and contacts of zoogeographical and physico-geographical principles of dividing territories into regions. He comes to the conclusion that division into regions according to the animal populations should be based on the study of the boundaries of their distribution. Besides this mode of zoogeographical division into regions there is another based on faunal regions whose taxonomical units are distinguished on the strength of their affinity.

THE ZOOGEOGRAPHICAL ASPECTS OF BIRD MIGRATION

Zoogeographers have always shown great interest in the migration of birds, their territorial distribution and the origin of migration. Therefore, it is no wonder that the representatives of faunogenetical zoogeography and also the specialists in territorial zonation have often made use of migration data to corroborate their theoretical assumptions.

As we know, in 1874 I.A.Palmén, an ornithologist working in Helsinki, published a book on the migration routes of birds, which caused a lively discussion and led to a great many additional investigations into the territorial distribution of bird migrations. As early as the middle of last century a Kiev Professor K.F.Kessler (1953) had written a long article on bird migration, in which he maintained that migrating birds would always fly along a broad front. In those days such a claim met with strong opposition from many scientists including Kessler's countrymen.

Academician A.Th.Middendorff (1855), who published a comprehensive survey of the results of the ornithophenological observations carried out in Europe and put forward a hypothesis contending that migrating birds were directed by the earth's magnetism, in one of the volumes of his "Siberian Journey" (1874) admits being a supporter of Palmén's theory and gives a large number of points of departure for the elucidation of this problem from the point of view of ecological zoogeography. At the end of the book Middendorff says that he has come to the same conclusions as Palmén on the strength of his own findings quite independently of the latter. A little later appeared the works by N.Y.Severtzow (1880) about the migratory birds of Central Asia and by M.A.Menzbier (1886) on the migration routes of birds in the European part of Russia, which on the basis of scanty factual material, mostly relying on their own theoretical speculations, gave a more exact scheme of the migratory routes suggested by Palmén making many corrections in them. It was probably the prestige of the above-mentioned great specialists in natural sciences that made later investigators try to adjust the results of their work to fit the theory of "migration routes". A large amount of literature was issued on

the subject and the influence of this theory is still to be felt even in the works of a number of present-day natural scientists.

M.A.Menzbier pays much attention to the problem of bird migration also in his "Ornithological Geography" (1882), in which he puts forth a hypothesis concerning the causes of this phenomenon and its connection with historical factors. This attractive theory found many supporters among the representatives of the future school of faunogenetical zoogeography in Russia.

M.A.Menzbier's last book (1934b) is specially devoted to the question of bird migration from the zoogeographical point of view. Up to the end of his long life he remained faithful to his theory of migration routes and staunchly defended the views that contemporary migration routes are the same as had been the historical routes of spread of the species. In this last book of his Menzbier raises and tries to solve many problems concerning bird migration which are still topical nowadays. It is not his fault that he did not have the necessary methods at his disposal and could not give answers to questions which only present-day investigators are able to clarify. First and foremost Menzbier was a zoogeographer with a strongly developed interest in the historical aspect, an evolutionist who tried to explain the problems he discussed from the point of view of their genesis and development.

We know that even today scientists keep arguing about the problem of whether birds migrate along migratory routes or on a broad front (Kumari, 1957). In recent times the theory of leading lines has eliminated many conflicting viewpoints from the theory of migratory routes (Kumari, 1971). Nowadays hardly anyone would dare to seriously defend the idea of "migratory routes" in the sense that they were presented by Palmén, Severtzow and Menzbier. Even today bird migration poses many zoogeographical problems (Kumari, 1959) the solution of which is being sought by the joint efforts of not only zoogeographers, but also ecologists, physiologists, ethologists, systematists and specialists in the history of sciences. Bird migration constitutes an extremely complicated biological problem which can only be solved through the collaboration of specialists in many fields. For this aim the study of the zoogeographical aspects of bird migration has not lost importance even today.

The most outstanding representative of faunogenetical zoogeography engaged in the study of bird migration is A.J.Tugarinov, who has written a number of separate articles on the subject (1937, 1950, 1952). He as well as other specialists in historical zoogeography are of the opinion that "migration routes" (the territorial distribution of migrations) may be evidence of the living conditions in the past, including the distribution of water and mainland. For instance, the migration of waterfowl across arid regions may be an indication of the existence of water bodies in those localities in the past, and in the same way the flight of land birds across seas may testify to the former existence of islands and peninsulas that have been submerged. Thus, the specialists in historical zoogeography regard the so-called "White Sea-Baltic migration route" of birds between the White and Baltic seas also as a "historical" one and not one chosen by them because of the present ecological conditions obtaining in the region.

With the increase of new ecological information in the works of Soviet zoogeographers and the accumulation of new factual materials the old ideas in the treatment of bird migration have given way to updated ones. Thus,

A.V.Mikheyev (1964) has given a good survey of the environmental factors influencing the seasonal migration of birds in the Eastern Palearctic region and of the territorial distribution of migration. E.I.Gavrilov (1979) has established the distribution of bird migration over the territory of Kazakhstan on the strength of copious factual material including the data of bird ringing collected at several points. Bird ringing carried out on a massive scale in the Baltic region during the post-war years has yielded a wealth of material for the solution of a wide variety of zoogeographical problems. Some results of this work are discussed in a book by E.Kumari (1975).

Abundant material for the development of ecological zoogeography has also been collected through research into the distribution of the wintering populations of the waterfowl, which have been systematically investigated in the Baltic region in recent times. A.O.Tashliyev (1975) has shown that palearctic birds have chosen new wintering territories including the man-made water reservoirs in Central Asia.

SOME SPECIAL PROBLEMS OF REGIONAL ZOOGEOGRAPHY

In every zoogeographical region, especially on such a vast territory as that of the Soviet Union, there are particular zoogeographical problems that can be solved successfully on the basis of regional materials. In the present concise survey only some of these can be discussed.

Interest in the origin of the fauna of the tundra was already taken by M.A.Menzbier. Later on much attention to zoogeographical problems connected with the Arctic region was paid by Soviet ornithologists. A.A.Kishchinsky (1980b) shows that on the basis of Arctic deserts and tundras (called provinces in the division of the Arctic region proposed by L.A.Portenko) the Arctic avifauna should be divided into two parts - the eoarctic faunal complex (or type) and the hypoarctic faunal complex (or type). The former populates the northern part, and the latter the southern part (the southern parts of the tundra, forest tundra and the northern belt of the taiga) of the Arctic region. Consequently, in the north of the Holarctic faunal region there are an eoarctic and a hypoarctic biogeographical zone, concepts which are more of a genetic character than concepts of landscape. Thorough research into the Arctic avifauna has been carried out by S.M.Uspensky (1969), who has shown that as a result of the recent rise in the temperature of the Arctic region a number of southern bird species have spread to the northern areas.

In the Soviet Baltic region intensive ornithological investigations have been going on for nearly two hundred years. This region is conspicuous for two leading directions in ornithological research: of the ornithofauna (Kumari, 1958) and bird migration. In recent years our ornithologists (O.Renno) have taken an active part in the compilation of ornithological atlases (Kumari, 1980).

In the south of the European part of USSR (and in Central Asia) an interesting faunogenetical problem is the origin and development of the bird fauna of the steppes. M.A.Voinstvensky (1960) proposes the division of the steppe zone of the European part of the USSR into a western and an eastern steppe region and a region of river valleys and littorals. The fauna of the European steppes has links with the fauna of the Palearctic deserts, although the present-day avifauna of the steppes possesses very few typically desert elements.

The steppe ornithofauna in the Palearctic region is characterized by endemism (Stegmann, 1955). According to the calculations by I.A.Dolgushin (1959) the Eurasian zonal steppes and forest steppes into one zoogeographical unit is not justified. The main centres of formation of the steppe bird fauna are to be found in Mongolia, Central Kazakhstan and Asia Minor. The fauna of the European steppes consists exclusively of species of Asiatic origin.

The bird fauna of the deserts of the Central Asian republics lives in peculiar and extreme conditions. A.K.Rustamov (1954) has shown in his investigations that most of the desert species were characteristic inhabitants of the deserts of the Western Palearctic region during the Miocene and Pliocene periods. Asia Minor and Central Asia constitute a relatively recent post-pliocene centre of formation of the desert fauna. More ancient centres of formation of the desert fauna are probably those situated in North Africa and the Central Asian Highlands. True, there really are to be found a considerable number of desert elements in the Central Asian Highlands, but here, too, they are of African origin (Kozlova, 1975).

A special survey of the bird fauna of the mountains of the Southern Palearctic region has been published by R.L.Böhme (1975), who claims that this territory should be distinguished as a separate zoogeographical unit (province). The avifauna here differs from all other avifaunas, which is to be explained by its origin resulting from the mountain-forming processes.

The Far East is an outlying region of the Palearctic with very interesting faunal peculiarities. For example, K.A.Vorobyov (1954) distinguishes five types in the bird fauna of the Ussurian territory (types after Stegman, who found only two types there): the Siberian, Chinese, Indo-Malayan, Mongolian and European types. The composition of this fauna is heterogeneous and very complicated. The most prominent proportion of its ornithofauna is made up of Siberian and Chinese elements. The Ussurian territory, which remained unaffected by the Ice Age, has preserved in its habitats a number of ancient, endemic species. E.N.Panov (1973), who explored Southern Primorye, discovered bird migration on a considerable scale here, too.

The ornithofauna of the Kurile Islands (Netchaev, 1969) is genetically closely linked to the bird fauna of the island of Hokkaido. The genetic links with Primorye, the island of Sakhalin, the Kamchatka peninsula, the Central and Southern Japanese islands appear to be much weaker. The ornithofauna of the Northern Kuriles is more similar to that of Kamchatka. In connection with the present warming of the climate a number of bird species that used to live farther to the south have been recorded as spreading to the South Kurile islands.

Very interesting ornithogeographical problems are connected with the extreme north-eastern corner of Asia, including the region of the Bering Sea. Far-reaching conclusions drawn from the results of his long-standing exploration in North-East Asia have been published by L.A.Portenko (1972, 1973). The most important of these are: the Arctic region constitutes a connecting link between the Palearctic and Nearctic regions; the Holarctic zoogeographical region consists of six subregions (the Sonorian, Canarian, Arctic, Siberian-European, Southern Palearctic and Chinese-Himalayan subregions); the exchange between the faunas of the Asian and American continents takes place in the region where they are nearest to each other (in that of the Bering

Strait); the ornithofauna of Eurasia and North America are most similar and possess the greatest number of common features in the northern and middle latitudes of both continents.

An important contribution to the scientific information concerning North-East Asia has been made by the investigations carried out by A.A.Kishchinsky (1980) in the Koryak Highlands. He has succeeded in establishing that the avifauna of the forest region in Kamchatka is being gradually ousted by the avifauna of the forest tundra of the Bering region. The birds of American origin in this region constitute a north-eastern tundra element. The palearctic elements have spread to the Anadyr-Koryak region from the west. The forest species have immigrated to the Koryak Highlands mostly from Kamchatka, and all the other avifaunal complexes here are also allochthonous.

Much argument and many conflicting views among zoogeographers have been caused by the question of the role played by the Bering Gulf and Sea in the mutual spread of the Palearctic and Nearctic birds. The width of this strait attains only 35-85 kilometres. Paleogeographers think that in the past between North-Eastern Asia and Alaska there was a hypothetical continent (Beringia), which formed a sort of "bridge" across which an exchange of the faunal elements took place. The idea of the existence of a former land connection between the two continents as an explanation of the ornithogeographic problems has been supported by B.K.Stegman (1967 and earlier works) and is opposed by L.A.Porstenko. The right view is perhaps held by A.A.Kishchinsky (1979), who says that our information on the present distribution of birds is not reliable enough to assert the existence of former land connection in the Bering region. Owing to its narrowness the Bering Strait does not constitute any obstacle preventing the spread of birds even without such hypothesis.

THE PROGRESS OF ECOLOGICAL STUDIES

Birds constitute excellent material for ecological studies and make splendid model species for the purpose. During the post-war years the ecological investigation into different bird species has made great progress in the USSR and at the present time there are specialists engaged in the study of almost all the main systematic groups of birds. Here we can only present the most general information concerning the trends of research and the extent to which the different groups of birds have been investigated.

The most thorough autecological studies have been made of those species that are of importance for the national economy: the gallinaceous birds, the waterfowl, and the hole-nesting birds. Monographs and a number of articles in different journals have been published on separate species. Autecological information is most easily available in such general surveys as Fauna of the USSR, and Fauna of the Union republics.

In the recent decades also a number of demecological investigations (concerned with population ecology) have been started. Here mention may be made of collections of articles devoted to one certain subject, papers delivered at conferences and other publications dealing with the waterfowl, gulls and some passerines. Demecological investigations are published in the works of the ornithologists of the Baltic region, Leningrad, Moscow, and also of some other regions of the Soviet Union.

Synecological studies are not so numerous. Bird counts have been taken and the interrelations of different bird species have been investigated in forest biocoenoses, and also in the case of the waterfowl, shore and sea birds. Recently the study of this subject gained momentum in connection with ecological monitoring.

Good bases for all sorts of ecological investigations are provided by the state nature reserves and the field stations of research institutes and higher educational establishments. Especially valuable information has been received from the year-long ecological observations of selected species and the biocoenological surveys made under projects IBP and MAB.

During the post-war years in the Soviet Union a large number of meetings for the discussion of ecological problems have been held as well as all-Union and regional zoogeographical and ornithological conferences, where questions of ecology have occupied the most prominent place. The journals "Ecology," "Ornithology" and "Zoological Journal" have printed a large number of articles dealing with problems of ecology and zoogeography. Scientific workers and students of the higher educational establishments of the Soviet Union are greatly interested in the ecological study of birds and every year there are many enthusiasts who readily undertake such investigations.

EFFLORESCENCE OF ECOLOGICAL ZOOGEOGRAPHY

The classical Soviet textbooks of zoogeography by V.G.Geptner (1936), I.I.Puzanov (1938), N.A.Bobrinsky, L.A.Zenkevich and J.A.Birstein (1946) consider N.A.Severtzov (1877) to be the founder of the ecological trend in Russian zoogeography. However, in those works, as in a number of others, no mention is made of A..Middendorff (1815-1894) one of the outstanding great zoogeographers of last century. During his journey through Siberia in 1842-1845 this remarkable specialist in natural sciences succeeded in collecting an enormous amount of factual material on the ecological causes of the distribution of the animals in the Eastern Palearctic region (Middendorff, 1853, 1874). Consequently, he considerably anticipated his contemporaries and actually it is he who should be regarded as the founder of ecological zoogeography in Russia (Kumari, 1978).

Many decades passed before an intensive development of ecological zoogeography began in the Soviet Union. Its great importance had already been admitted by Geptner, however, it was not until the beginning of the 1950s that the ecological factors influencing the distribution of animals came to be regarded as the most important ones. At the same time Soviet zoogeographers lost interest in historical zoogeography and at the present time only a few scientists are dealing with it (Kishchinsky, 1977).

S.S.Schwarz is of the opinion that within the limits of one region, subregion or province the representative of separate faunal complexes differ from each other not only as regards their history of spreading, but also as concerns their general ecological peculiarities. Therefore, research into the ecological peculiarities of the representatives of different faunal complexes is both of interest in itself and also of great importance for the study of the history of the formation of different faunas.

In the comprehensive ornithofaunistical surveys published nowadays about various parts of the USSR the ecological factor in the distribution of birds

is considered to be of great importance. Present-day Soviet ornithogeography is actually ecological zoogeography. To give a few examples of the application of landscape, ecological and biocoenotic factors and concepts in avifaunistic studies, mention may be made of the works by A.N. Formozov (1937) on the waterfowl in the Naurzum nature reserve, by S.V. Kirikov (1952) about the birds and mammals of the Southern Urals, by F.I. Strautman (1954) on the birds of the Soviet Carpathians, by E.M. Vorontzov (1954) on the bird communities inhabiting the mixed forests of the European part of the USSR, by A.K. Rustamov (1954) on the birds of the Kara-Kum desert, by M.S. Dolbik (1974) on the ornithofauna of Byelorussia, by J.S. Ravkin (1978) on the birds inhabiting the forest zone in the region of the river Ob, and many others.

A large amount of literature has appeared about the ornithofauna of man-made landscapes and the problems connected with them. Human activities in different landscape areas and their impact on the distribution of separate species and whole faunal complexes have been dealt with from a wide variety of aspects. An attempt has been made to treat the problem against the background of the changes that have taken place in the forest steppes of Eastern Europe in the course of the last ten centuries (Kirikov, 1979).

For the last decades the favourite subject of many Soviet ornithologists has been the dynamics of the ornithofauna and its two most important causes - the changes in the landscapes under the impact of human activities and the fluctuations of the climate. A separate article has been devoted to the effect of the severe winter of 1939/1940 on birds (Dementiev, Shimbireva, 1941). The dynamics of the ornithofauna under the influence of the above-mentioned factors have been studied in the Baltic region (Kumari, 1957, 1966) as well as in the Ukraine (Scharkman, 1960; Andrievsky, Treus, 1961), in Central Asia (Varschavsky, 1963; Ryabov, 1974) and in Siberia (Rogacheva, Syroetchkovsky, 1962).

V.A. Popov and A.K. Rustamov (1970) find that it is indispensable to create a special new field (or branch) of zoogeography - anthropogenetic zoogeography, which would investigate the changes in the distribution of animals under the influence of man's many-sided activities, the laws governing these influences and the ways in which they make themselves felt. This kind of zoogeography would be of great practical importance. A special book written by D.V. Vladyshevsky (1975) on birds in man-made landscapes discusses the ecological bases of the existence of the bird species and complexes of bird species in this rapidly expanding type of landscape in the USSR.

AT THE SOURCES OF SYNTHETICAL ORNITHO GEOGRAPHY

In Soviet zoogeography there are two main trends - historical (faunogenetical) and ecological (landscape) zoogeography, both of which have their place and importance in the research into the distribution of birds in time as well as in space. At present it is difficult to imagine the independent, "pure" development of either direction. Mutual links leading to reciprocal enrichment through the adoption of each other's results and methods of work is the only correct approach to ensure the development of our ornithogeography. Without doubt A.A. Nasimovich (1967) was right in pointing out that the division of zoogeography into different trends is purely conditional: many investigators combine in their work the approaches and methods characteristic of zoogeographers of a variety of schools and trends.

In present-day Soviet zoogeography much attention is paid to animal populations and quantitative methods of research into them. Population ecology of birds has become part and parcel of the study of the geographical distribution of birds. Not only the boundaries of ranges and their fluctuations, but also the distribution of species and faunal complexes within the ranges have become subjects of zoogeographical investigations. That has led to new approaches to the research into bird communities.

A number of conferences have been held and numerous collections of articles have been published on the methods used in counting bird populations and compiling maps of their distribution. This has been done in the case of waterfowl, waders, hole-nesting passerines and several others. Works have appeared on the results of research into the structure of the distribution areas of bird species including the wintering populations of the waterfowl.

A.A.Nasimovich (1967) mentions one more trend in Soviet zoogeography - the biocoenological one, which is still in the process of formation. Discussing some of the trends of the development in present-day biogeography, A.G.Voronov (1980) raises the question of boundaries between biogeographical and ecological investigations. He points out that biocoenology covers the fields of ecology and biogeography. Nowadays research into the dynamics of communities has become one of the most important tasks of biogeography. Its objects of study are the fauna on the one hand, and animal communities on the other hand.

A promising trend in Soviet biogeography is the geography of animal resources, which is of importance for the development of the national economy and the conservation of the natural environment. Systematic work is also being done to improve the methods and devices applied in zoogeographical cartography.

In recent times there has appeared a tendency to unite the different directions in biogeography into a single science - synthetical biogeography (P.B.Vtorov, 1980 and a number of earlier works). In this author's opinion owing to the general tendency towards the ecologization of many of the natural sciences, which is a logical and useful process, preconditions have been created for investigating the living nature from integrated points of view. The synthetical tendencies in biogeography must be balanced with tendencies of an analytical character. An important task of synthetical biogeography is the study of ecosystems and communities. These should be investigated by means of quantitative counts of most groups of organisms, making an especially detailed analysis of some key groups.

The research into the bird fauna and its communities has proved that integration of the tasks and methods of faunogenetical and ecological zoogeography (ornithogeography) is quite possible and in a number of cases indispensable. At the same time, we cannot deny the applicability of classical historical zoogeography, in which biogeographical methods play a useful role in reconstructing the history of the avifauna (Kistchinsky, 1977).

A number of the principles of classical zoogeography have been subjected to justified criticism over the last few decades. Attention has been called to the fact that distinction should be made between the concepts "fauna" and "animal community", as well as between the synecological, geozoological and faunogenetical approaches (Chernov, 1975). All these problems have to be solved by contemporary science. But the roots of Soviet ornithogeography lie in the achievements of the preceding generations of our ornithologists and zoogeograp-

hers, whom we esteem highly and from whom we take over the valuable part of their work, which cannot be devalued by either the lapse of time or shift in space.

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THE PHYLOGENY AND CLASSIFICATION OF THE PASSERINE BIRDS,
BASED ON COMPARISONS OF THE GENETIC MATERIAL, DNA

Charles G. Sibley and Jon E. Ahlquist

Department of Biology and Peabody Museum of Natural History,
Yale University, New Haven, Connecticut 06511, U.S.A.

Introduction

The order Passeriformes contains 5274 (=58.5%) of the 9021 species of Recent birds (Bock and Farrand, 1980). Thus it is, by far, the largest order of birds and the "vexed question" of its division into families, that troubled Sclater (1880) a century ago, remains unsolved in spite of the efforts of many avian systematists. Sibley (1970) reviewed the history of passerine classification and the numerous proposals concerning the relationships among passerine taxa. The electrophoretic comparisons of the egg white proteins presented in that study also did little to advance our knowledge of passerine phylogeny, although they did "suggest that larger assemblages than have been recognized may exist" (1970:111).

Since 1950, the remarkable discoveries in molecular biology have been accompanied by the development of new techniques which make it possible to compare the genes themselves. The fact that the genetic material, DNA, proved to be a double-stranded molecule, composed of two complementary sequences of the four genetic coding units, the nucleotides, resulted in the development of the technique of DNA-DNA hybridization which permits us to compare the DNAs of any two birds. From its beginnings in the 1960's (e.g. Schildkraut et al., 1961; Hoyer et al., 1964; Britten and Kohne, 1968) the DNA hybridization technique was brought to a high level of competence in the 1970's (e.g. Kohne, 1970; Kohne and Britten, 1971; Britten et al., 1974).

We first tried to use DNA hybridization for avian systematics in 1963, with the generous help of several of the pioneers, including Ellis Bolton, Bill Hoyer, and Brian McCarthy. We failed at that time because of technical problems but, in 1973, after Shields and Straus (1975) had used improved methods in a successful study of avian DNAs, we resumed research with DNA hybridization. By early 1975 we were able to produce large numbers of DNA-DNA comparisons and since then we have examined over 16,000 DNA-DNA hybrids among avian taxa, about 10,000 of them between passerine species. From these data we have been able to reconstruct the phylogeny of the Passeriformes down to the level of tribes. We have compared members of all but six of the 70 passerine "families" recognized by Wetmore (1960), and at least three of those six have been shown to be members of other families (Hypositta=Vangidae, Dorst 1960; Zeledonia=Fringillidae: Parulini, Sibley 1968; Phytotoma=Tyrannidae: Cotinginae, Sibley and Ahlquist in press b). The missing Wetmore families are Philepittidae, Vangidae, and Callaeidae.

Methods

Our DNA-DNA hybridization procedures are based upon those of Britten and Kohne (1968), Kohne (1970), Kohne and Britten (1971), and Britten et al. (1974). In other publications we have described our methods in moderate detail (Sibley and Ahlquist

1981a; 1983) and briefly (Sibley and Ahlquist 1980; 1981 b,c; 1982 a-e, i; Sibley et al., 1982). The following synopsis is modified from Sibley and Ahlquist (1982 b,c).

DNA is a double-stranded molecule composed of linear sequences of four types of nucleotides which differ in the structure of their "bases," namely, adenine (A), thymine (B), guanine (G), and cytosine (C). In double-stranded DNA the bases occur as complementary pairs: an A in one strand pairs only with a T in the other strand, a G pairs only with a C. Genetic information is encoded in the sequence of the bases. The two strands of DNA will separate if heated in solution to ca. 100°C which dissociates ("melts") the hydrogen bonds between base pairs. When cooled the double-stranded molecule reforms because the complementary base pairs reassociate. If the temperature is maintained at or above ca. 60°C base pairing will occur only between long homologous sequences of bases. This is because only long sequences of complementary bases have sufficient total bonding strength to maintain stable duplexes at such temperatures, and only homologous sequences possess the necessary degree of complementarity. Thus, under appropriate conditions, the single strands of conspecific DNA will reassociate with their homologous partners and the matching of complementary bases will be essentially perfect.

Similarly, if the single-stranded DNAs of two different species are combined under conditions favoring reassociation, "hybrid" double-stranded molecules will form between homologous sequences. These hybrid duplexes will contain mismatched base pairs because of the base sequence differences that have evolved since the two species diverged from their most recent common ancestor. Since mismatched bases (e.g. A-G, C-T) do not form hydrogen bonds between them, the total bonding strength of DNA hybrid molecules is less than that of conspecific double-stranded DNA. This causes the hybrid molecules to melt at a temperature lower than that required to dissociate conspecific duplexes. These facts are the basis of the DNA-DNA hybridization technique. At 60°C the base pairs must be at least 80% correctly matched to form a stable duplex molecule.

The extent of base pair complementarity between the homologous base sequences of any two DNAs can be determined by measuring (1) the percentage of the two DNAs that form hybrid molecules at a given temperature, e.g. 60°C, and (2) the thermal stability (i.e., melting temperature) of the hybrid molecules. These properties may be determined, as follows.

DNA is obtained from cell nuclei and the proteins and ribonucleic acids (RNAs) are removed. The purified DNA is then "sheared" into fragments with an average length of 500 bases. For a given set of comparisons, the single-stranded DNA fragments of one species must be "labeled" with a radioactive isotope, such as Iodine-125 (^{125}I). To achieve reproducible results, and to obtain a true measure of nucleotide sequence evolution, it is necessary to remove most of the copies of repeated sequences from the DNA of the species to be labeled, thus producing a "single-copy tracer" DNA. This is accomplished by allowing the single-stranded DNA of the tracer species to reassociate until most of the identical repeated sequences, which reassociate rapidly, have formed double-stranded molecules. The single-copy sequences remain single-stranded and may then be recovered by chromatography on a

hydroxyapatite (HAP) column, which separates single-stranded from double-stranded DNA. This process produces a single-copy DNA preparation consisting of one copy per genome of each original single-copy sequence, plus at least one copy per genome of each different repeated sequence. Such a preparation contains at least 98%, and probably 100%, of the different DNA sequences (Britten,1971).

The single-copy preparation is then labeled with radioiodine (¹²⁵I) to produce a "tracer" and DNA-DNA hybrids are formed by combining one part of the single-copy tracer DNA with 1000 parts of the sheared, whole, "driver" DNAs of other species. For example, in a study of the relationships of the accentors (Prunella) we prepared an experimental set including the following taxa (Sibley and Ahlquist,1981b).

| Radio-labeled Species | | | Unlabeled Species | |
|----------------------------|---|---|-----------------------------|-------------------------------------|
| <u>250 ng "tracer" DNA</u> | | | <u>250 µg "driver" DNA</u> | <u>Δ T₅₀^H</u> |
| Prunella modularis | | x | <u>Prunella modularis</u> | 0.0 |
| " | " | x | <u>Prunella atrogularis</u> | 1.9 |
| " | " | x | <u>Ploceus capensis</u> | 7.0 |
| " | " | x | <u>Anthus trivialis</u> | 8.4 |
| " | " | x | <u>Carduelis spinus</u> | 9.7 |
| " | " | x | <u>Sturnus vulgaris</u> | 10.1 |
| " | " | x | <u>Turdus migratorius</u> | 11.9 |

The hybrid combinations are placed in vials and heated to 100°C for 5 minutes to dissociate the DNAs into single-strands, then incubated for 120 hours at 60°C to permit the formation of double-stranded molecules. The DNA hybrids are then placed on hydroxyapatite columns in a temperature-controlled water bath at 55°C and the temperature is raised in 2.5°C increments from 55°C to 95°C. At each of the 17 temperatures the single-stranded DNA produced by the melting of the double-stranded molecules is washed from each column in 20 ml of 0.12 M sodium phosphate buffer.

The amount of radioactivity in each sample is then measured and these data are used to calculate the average melting temperature of each DNA hybrid. To compare the genetic similarity between species we use a single number statistic, the T₅₀^H (Kohne,1970:349; Bonner et al.,1981; Sibley and Ahlquist,1981a). The calculation of T₅₀^H assumes that all of the sequences in the two genomes being compared have homologs in the other species, that all homologous sequences can form hybrid duplexes, and that all degrees of divergence can be detected. The T₅₀^H is the temperature in degrees Celsius at which 50% of all actual or potential DNA duplex molecules have dissociated and it therefore measures the average genetic divergence between the two taxa forming a DNA-DNA hybrid.

In each experimental set the radio-labeled tracer species (e.g. Prunella modularis) is hybridized with itself (=homoduplex) and the differences in degrees Celsius between its T₅₀^H value (=0.0), and those of each of the heteroduplex hybrids, are the delta T₅₀^H values (e.g. 1.9, 7.0, 8.4, etc.). A delta value of 1°C is produced by a base pair mismatch of ca. 1% between the genomes of the two species forming a DNA-DNA hybrid (Bonner et al.,1973).

In several papers we have presented evidence showing that delta T₅₀^H values are

measures of the average rate of DNA evolution (i.e., nucleotide substitution), and that the same average rate occurs in all avian lineages (Sibley and Ahlquist, 1981a, 1982a, 1983, in press a, b; Sibley et al., 1982). Thus the $\Delta T_{50}H$ values are measures of the relative times of divergence between the lineages represented by the species composing a DNA-DNA hybrid. From an earlier calibration of $\Delta T_{50}H$ values against absolute time we estimated that $\Delta T_{50}H$ 1.0 is equivalent to ca. 5 million years (my) since the time of divergence (Sibley and Ahlquist, 1981a: 322-323). This was based on the assumption that the common ancestor of the ostrich and the rheas was separated into African and South American populations by the opening of the Atlantic ca. 80 mya. Recent re-evaluation of these data indicate that a calibration of $\Delta T_{50}H$ 1.0 is closer to 4.5 my. This calibration seems reasonable for divergence dates older than ca. 60 my, but during the first 60 my after divergence the relationship between delta values and time seems to be curvilinear, possibly due to the changing probabilities of back mutations, multiple changes at the same nucleotide position, and the formation of new repeated DNA sequences. During the first 20 my after divergence the calibration seems to change as follows: $\Delta 1.0=2\text{my}$; $\Delta 2.0=5\text{my}$; $\Delta 3.0=9\text{my}$; $\Delta 4.0=13\text{my}$; $\Delta 5.0=18\text{my}$. Beyond 20 my the values are $\Delta 7.3=30\text{my}$; $\Delta 9.3=40\text{my}$; $\Delta 11.3=50\text{my}$; $\Delta 13.3=60\text{my}$; $\Delta 16=70\text{my}$; $\Delta 18=80\text{my}$; $\Delta 20=90\text{my}$; and $\Delta 22=100\text{my}$. These calibrations are tentative, preliminary, and subject to revision as more data are obtained. However, even if these absolute time values prove to be erroneous, the $\Delta T_{50}H$ values are valid indicators of relative time and we will use the above scale in this paper to provide estimates of divergence dates.

The data in this paper are based upon comparisons among ca. 800 species of passerine birds, of which ca. 200 are suboscines (Oligomyodi) and 600 are oscines (Passeres). About 150 species have been "labeled" with radioiodine and used as "tracers."

The ca. 10,000 $\Delta T_{50}H$ values have been entered in several matrices and the phylogeny has been developed by using the average linkage procedure described by Sibley and Ahlquist (1981a:313-314). The average $\Delta T_{50}H$ values in the phylograms are the products of this procedure. A $\Delta T_{50}H$ value of, for example, 6.3, may also be written as $\Delta T_{50}H$ 6.3, as $\Delta 6.3$, as 6.3, or as (6.3).

The phylogeny of the Passeriformes is depicted in Figures 1-20 and our classification is presented in Appendix. The categories Infraorder and Parvorder follow McKenna (1975).

Classification

The classification presented in this paper is based upon the phylogeny developed from the DNA-DNA comparisons.

The derivation of a classification from a phylogeny depends upon the taxonomic philosophy of the classifier. We agree with Hennig (1966) that, ideally, a classification should reflect the branching pattern of the phylogeny, that categorical rank should be determined by the age of origin of taxa, and that sister groups should be of coordinate rank. We also accept the proposal by Nelson (1973) to use the principles of "subordination and sequencing" and we agree with

Griffiths (1973:340-341) that it is neither possible nor important to attempt to express "evolutionary grades" of morphological characters as judged by the human eye or by measurements that bear "few relationships to other attributes of the taxa...."

We also believe that the data of DNA hybridization provide the "satisfactory general measure of evolutionary differentiation" which Griffiths (1973:338) considered to be "the central problem of evolutionary classification." A classification derived from DNA-DNA hybridization values will express degrees of genetic divergence which are, surely, the best general measure of evolutionary differentiation.

Although the DNA hybridization technique provides valuable new data for systematics it is a relatively complex procedure and experimental errors reduce the accuracy of single comparisons. It is therefore important to use multiple replicates and/or several species in each monophyletic cluster to obtain accurate average $\Delta T_{50}H$ values for divergence nodes (Sibley and Ahlquist 1983). Also, until at least one species in each cluster of closely related taxa has been radio-labeled, and compared with members of other such clusters, it is difficult to be certain of the branching pattern. These constraints increase the time and work required, but accurate average nodal values can be obtained and used to reconstruct the phylogeny of living taxa.

Because the $\Delta T_{50}H$ values are measures of divergence times between lineages it has been possible to apply Hennig's principle that categorical rank should reflect the time of origin. However, we cannot apply the Hennigian principle that every dichotomy should result in new categorical names for the resultant sister groups. The DNA-DNA phylogenies are too complex to make it practical to follow this rule in detail so we have compromised by dividing the geological time scale into segments and using the $\Delta T_{50}H$ scale to assign categories, as follows: Up to $\Delta 4.0$ (ca. 15 my)= congeners or closely related genera; $\Delta 4-7$ (ca. 15-30 my)= Tribe; $\Delta 7-9$ (ca. 30-40 my) = Subfamily; $\Delta 9-11$ (ca. 40-50 my) = Family; $\Delta 11-13$ (ca. 50-60 my) = Superfamily; $\Delta 13-15$ (ca. 60-70 my) = Parvorder; $\Delta 15-18$ (ca. 70-80 my) = Infraorder; $\Delta 18-20$ (ca. 80-90 my) = Suborder; $\Delta 20-22$ (ca. 90-100 my) = Order. We have tried to be consistent but it has been necessary to be flexible and the boundaries of categories have been allowed a variation of ± 1.0 $\Delta T_{50}H$ or $\pm 4-5$ my. Thus our classification reflects the phylogeny, but only the phylograms show the detailed cladistic patterns revealed by the DNA-DNA measurements.

The Suborders of the Passeriformes

Since 1847, when Johannes Müller discovered the morphological complexity of the avian syrinx, the major subdivisions of the Passeriformes have been based, in part, upon syringeal characters. Sibley (1970:23-31) and Ames (1971:127-129; 153-164) have reviewed the history of passerine systematics with special reference to the syrinx as the basis for the recognition of subordinal groups.

The influential classifications of Mayr and Amadon (1951), and Wetmore (1960), recognized four suborders: Eurylaimi, Tyranni, Menurae, and Oscines or Passeres. Ames (1971:153) added a fifth suborder, the Furnarii, but Olson (1971) recognized only three, Tyranni, Menurae, and Oscines, and he placed the Eurylaimidae in the

Tyranni because he believed them to be most closely related to the Cotingidae. Olson (1971) found that Menura has a ball-and-socket jaw articulation like that of the oscines, and unlike that of the suboscines. However, he retained the suborder Menurae while expressing the "opinion that they will ultimately be found to be closer to the Oscines than to the Tyranni."

The validity of subordinal rank for the lyrebirds (Menura) was challenged by Sibley (1974) and Feduccia (1975), both of whom concluded that Menura is oscine. Our DNA-DNA data support this conclusion and show that Menura is most closely related to the scrub-birds (Atrichornis) and the bowerbirds (Ptilonorhynchidae), as indicated in Figs. 2-4. We disagree with the conclusion by Feduccia and Olson (1982) that the lyrebirds and bowerbirds are not related (see Sibley and Ahlquist in press b).

The DNA hybridization data indicate that the four or five "suborders" noted above are not of equal rank and their recognition would violate the principles of a cladistic, dichotomous classification. We propose that the Passeriformes be divided into two suborders, the Oligomyodi containing the suboscines, and the Passeres (or Polymyodi) containing the oscines. These two suborders are well separated by anatomical characters and DNA-DNA distances. They diverged ca. 85-90 million years ago (mya) (Sibley et al., 1982; Sibley and Ahlquist, in press b). See Fig. 1.

The Subdivisions of the Oligomyodi

In most recent classifications the broadbills (Eurylaimidae) have been separated from the other suboscines because of several distinctive morphological characters (Olson 1971), and the pittas (Pittidae), philepittas (Philepittidae) and New Zealand wrens (Acanthisittidae) have been placed with the New World tyrannoids (Mayr and Amadon 1951; Wetmore 1960). Olson (1971) proposed that the Eurylaimidae and Philepittidae should be placed in the "Tyrannoidea" of Wetmore (1960), and that the Pittidae and Acanthisittidae should be treated as "Tyranni incertae sedis."

The DNA hybridization data have revealed a phylogeny that differs from all previous arrangements. Sibley et al. (1982), Sibley and Ahlquist (in press b), and Sibley et al. (in press) have compared the DNAs of all suboscine groups except the Philepittidae and Phytotoma, and the results are presented in Figure 1 and Appendix 1. They may be summarized, as follows:

1. The New Zealand Wrens are the descendants of the oldest known branch (ca. 80 mya) in the suboscine phylogeny. The infraorder Acanthisittides is therefore the sister group of all other suboscines.
2. The infraorder Eurylaimi includes the Pittidae and Eurylaimidae, and probably the Philepittidae.
3. The infraorder Tyrannides includes only the New World suboscines, which are divided into three parvorders.

a. Tyranni. The Tyrannidae of Wetmore (1960) is divisible into the Mionectidae, which consists of several genera previously thought to be typical tyrannids (e.g. Mionectes, Leptopogon, Corythopsis,

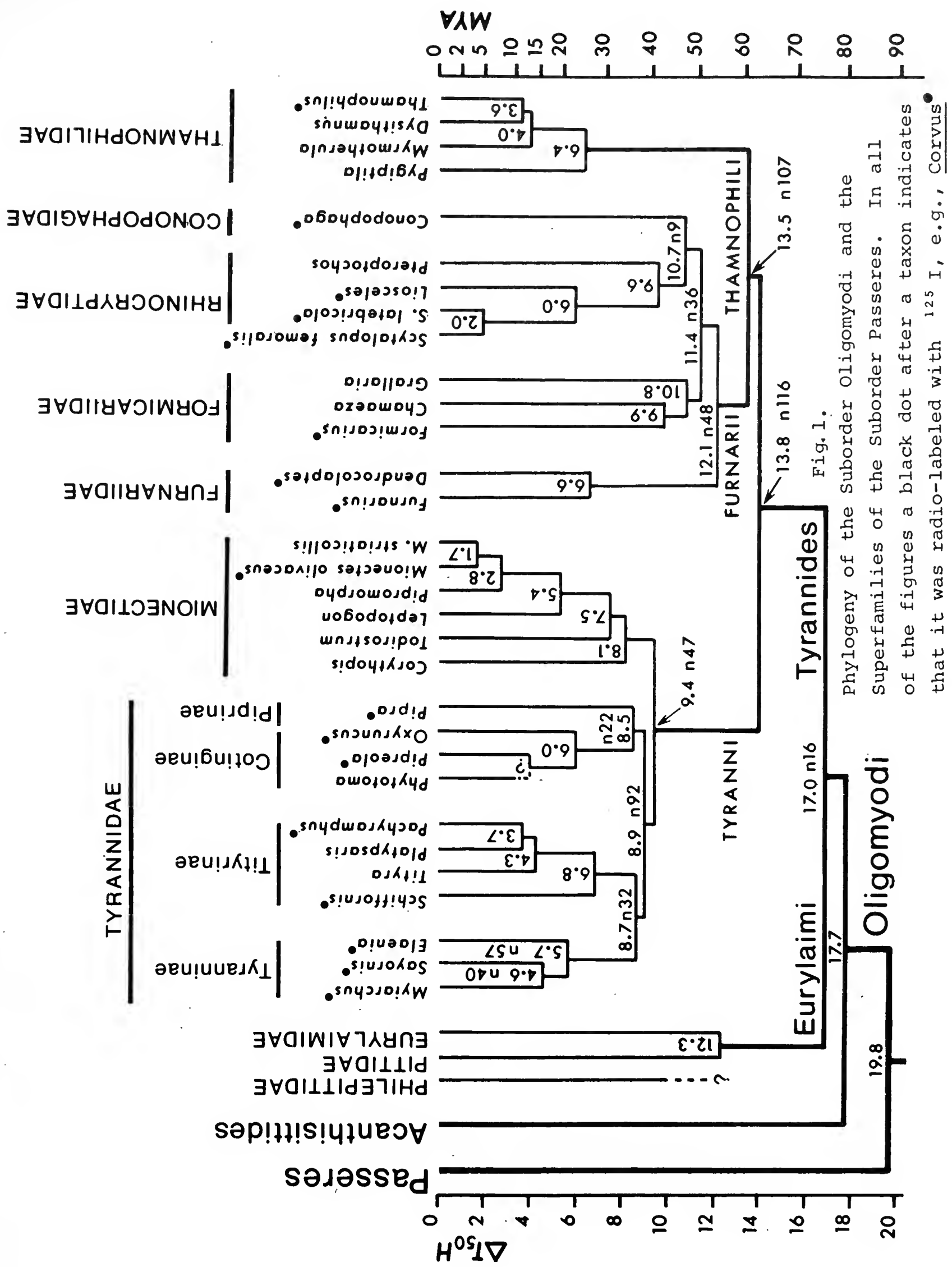


Fig. 1.

Phylogeny of the Suborder Oligomyodi and the Superfamilies of the Suborder Passeres. In all of the figures a black dot after a taxon indicates that it was radio-labeled with ¹²⁵I, e.g., *Corvus*.

Todirostrum), and the Tyrannidae which includes the Tyranninae, Tityrinae (incl. Schiffornis) Cotinginae (incl. Phytotoma, Oxyruncus), and the Piprinae. Sibley et al. (in press) have found that Oxyruncus is a cotinga and consider Phytotoma also to be a cotinga.

b. Furnarii. The Furnarioidea includes only the Furnariidae, the ovenbirds and woodcreepers. The Formicarioidea includes three families. The Formicariidae are the "ground antbirds," including Formicarius, Grallaria, Chamaeza, Pittasoma, and possibly others. The other formicarioids are the gnateaters (Conopophagidae) and the tapaculos (Rhinocryptidae).

c. Thamnophili. The ca. 44 genera of "typical antbirds" (e.g. Thamnophilus, Taraba, Dysithamnus) are the descendants of a lineage that diverged from the Furnarii before the furnarioids and formicarioids diverged from one another.

The DNA hybridization data are congruent with the morphological characters studied by Heimerdinger and Ames (1967), Ames et al. (1968), and Warter (1965). They agree well with Traylor (1977) and Snow (1973).

The Suborder Passeres

According to Bock and Farrand (1980) the suborder Passeres contains 4177 species in 823 genera. Sibley (1970:41-48) reviewed the taxonomic history and the characters that have been used to divide this large group into families and noted the range of opinion expressed by different systematists concerning the number of families to be recognized. Stresemann (1934) arranged the group in 49 families, Mayr and Amadon (1951) in 36, Mayr and Greenway (1956) in 40, Amadon (1957) in 42, Delacour and Vaurie (1957) in 39, and Wetmore (1960) in 54. These six treatments range from 36 to 54 families and average 41, suggesting that a reasonable consensus had been achieved during the period from ca. 1930 to 1960. This consensus has now been broken by the classification of Wolters (1975-1982) which recognizes 91 families of Passeres, and by the classification presented in this paper in which we include the same taxa in 27 families. However, we recognize many of the same groups at the subfamilial and tribal levels. One reason for the discrepancy is that the DNA hybridization data provide an index to the dimension of time and thus permit us to realize Hennig's (1966:160) hope that the age of origin could be used as the basis for an absolute ranking of taxa. We have discussed this subject elsewhere (Sibley and Ahlquist, 1982d).

The sequence of families to be followed in a linear list that would express an evolutionary lineage from "primitive" to "advanced" has also produced disagreements (Mayr and Greenway, 1956; Wetmore, 1957; Mayr, 1958; Storer, 1959). Our sequence is derived from the DNA phylogeny and reflects the principles suggested by Nelson (1973).

Many of the earlier classifications of the Passeres have been lists of "families" with little or no hierarchical structure and only that of Wolters is based on cladistic principles. Wetmore's (1960) classification is merely a list of 54 "families" with no other categories below the suborder. Mayr and Amadon (1951)

recognized a series of "vernacular groupings...to aid in associating related families" and used subfamilies and tribes to provide additional hierarchical structure. Beecher's (1953) attempt to develop a phylogeny of the oscines, based primarily on the jaw musculature, was not successful and the other classifications have been based mainly upon external morphology and the impressions derived from long experience with museum specimens.

We may therefore begin, with few prior constraints, to develop a phylogeny from the ca. 8000 DNA-DNA comparisons we have made among oscine taxa.

The Major Subdivisions of the Passeres

The DNA data reveal two major groups within the Passeres which we recognize as the Parvorders Corvi and Muscicapae, each subdivided into three Superfamilies.

The Corvi and Muscicapae diverged ca. 55-60 mya, in the Paleocene. Most of the living Corvi are confined to Australasia and it seems clear that the group originated in Australia because the oldest elements are still confined to Australia and New Guinea. These are the lyrebirds (Menura), scrub-birds (Atrichornis), bowerbirds (Ptilonorhynchidae), and treecreepers (Climacteridae) of the Superfamily Menuroidea, the fairy-wrens (Maluridae), honeyeaters (Meliphagidae), and Australian warblers (Acanthizidae) of the Superfamily Meliphagoidea, and most of the many groups forming the Superfamily Corvoidea. Figures 2 to 11 present the phylogeny of the Corvi.

One of the surprises revealed by the DNA comparisons is that the bowerbirds are not closely related to the birds-of-paradise. Instead, the bowerbirds are the sister group of the lyrebirds and scrub-birds (Menuridae) and the birds-of-paradise are related most closely to the Australo-Papuan magpies and butcherbirds (Cracticini). The lyrebirds and bowerbirds are similar in other characters including display behavior, breeding systems, delayed development of male plumages, vocal mimicry, and the electrophoretic patterns of their egg white proteins. Sibley (1974) reviewed these shared characters and concluded that the total available evidence indicated that "Menura is more closely related to the bowerbirds than to the birds-of-paradise, although all three groups are members of a single natural cluster." The DNA data have confirmed this conclusion and have added additional details to our understanding of the relationships among these taxa.

The fact that the lyrebirds branched from the bowerbirds at $\Delta T_{50}H$ 9.9 (ca. 40-45 mya), and that the Corvi branched from the other oscines at $\Delta T_{50}H$ 13.0 (ca. 55-60 mya) shows that the syringeal characters of Menura are derived, not primitive.

Feduccia and Olson (1982) interpreted the convergent similarities in several morphological characters as evidence of relationship between the suboscine Rhinocryptidae and Menura. They also argued that skeletal differences between Menura and the bowerbirds proved that the two groups are not related. The DNA hybridization measurements indicate that these opinions are erroneous.

Preliminary DNA comparisons indicated that the Australo-Papuan treecreepers (Climacteris) are related to the lyrebird-bowerbird group. This was so surprising that additional material was obtained and an extensive study was made. The earlier

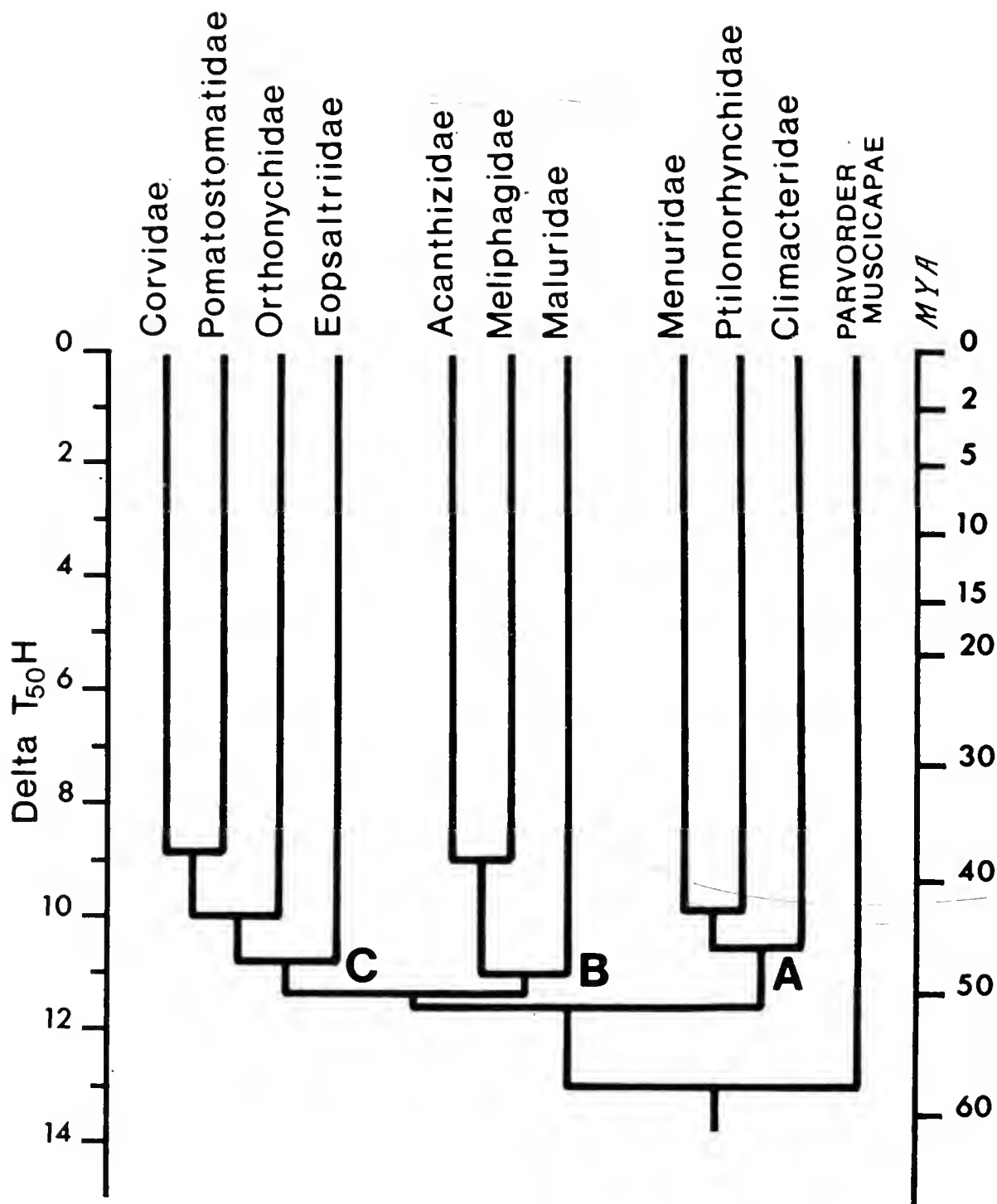


Fig.2. Families of the Parvorder Corvi. Group A-Superfamily Menuroidea, B-Meliphagoidea, C-Corvoidea

results were confirmed and the data show that the treecreepers are the descendants of the earliest branch in the Menuroidea at delta T₅₀H 10.4, ca. 45-50 mya (Sibley, Schodde, and Ahlquist, in press). Harrison (1969) and Parker (1982) favored the Meliphagidae as the closest relatives of Climacteris, and Orenstein (1977:224-8) suggested that Climacteris may represent "a distinct branch of a major Australian radiation...."

Although Climacteris is morphologically distinct from Menura and the bowerbirds, it is superficially similar to Atrichornis in size, coloration, bill shape, and nasal opercula. These characters may mean little but they suggest that additional evidence of this relationship may be found.

The fairy-wrens (Malurus), emu-wrens (Stipiturus), and grasswrens (Amytornis) of the Maluridae have often been included in the Sylviidae but the DNA data show that they are the sister group of the Australian warblers (Acanthizidae) and honeyeaters (Meliphagidae) from which they branched ca. 48-50 mya (Sibley and Ahlquist, 1982h).

The Meliphagidae includes the Australian chats Ephthianura and Ashbyia which, the DNA data indicate, are actually more closely related to such typical

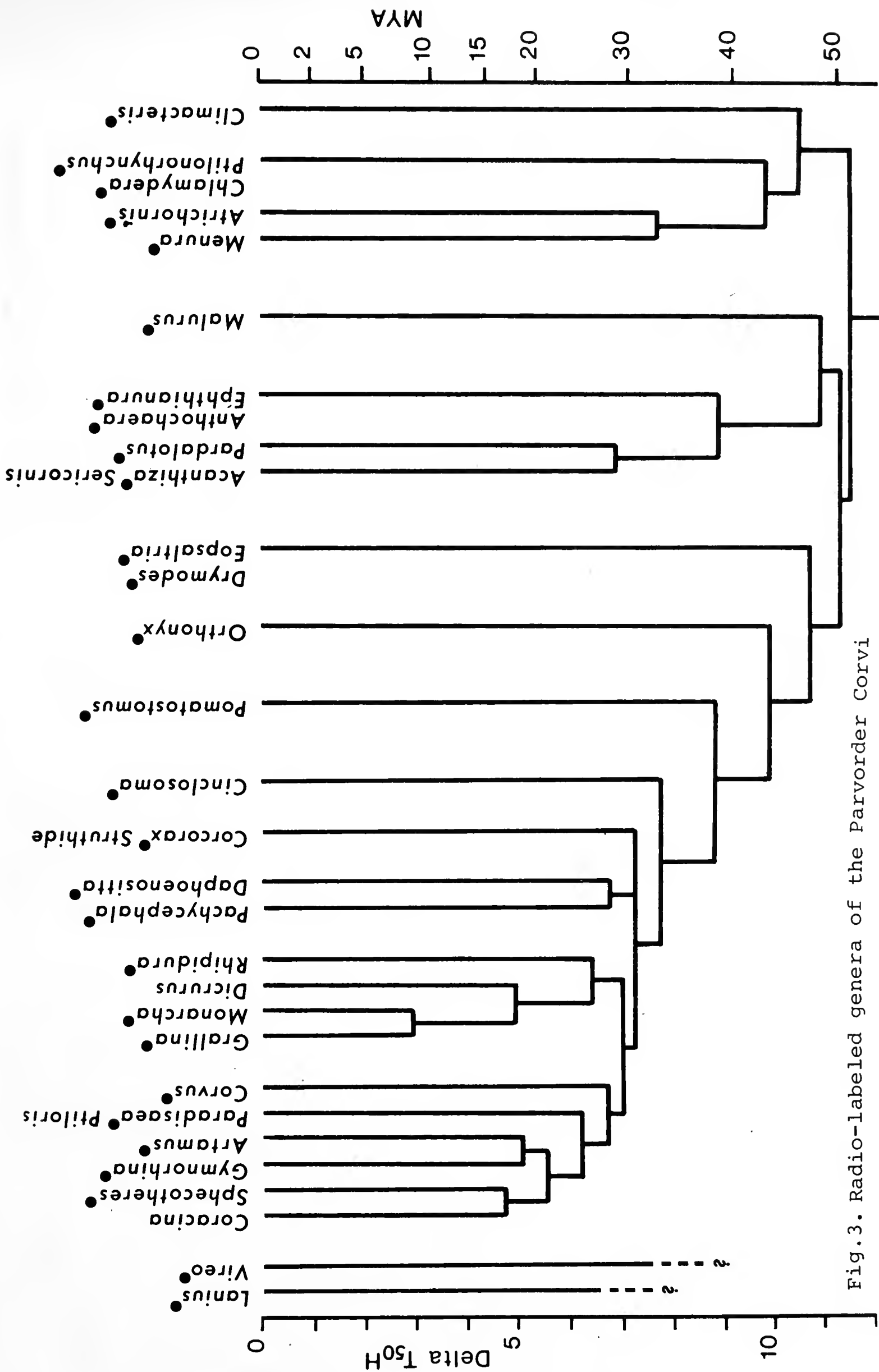


Fig.3. Radio-labeled genera of the Parvorder Corvi

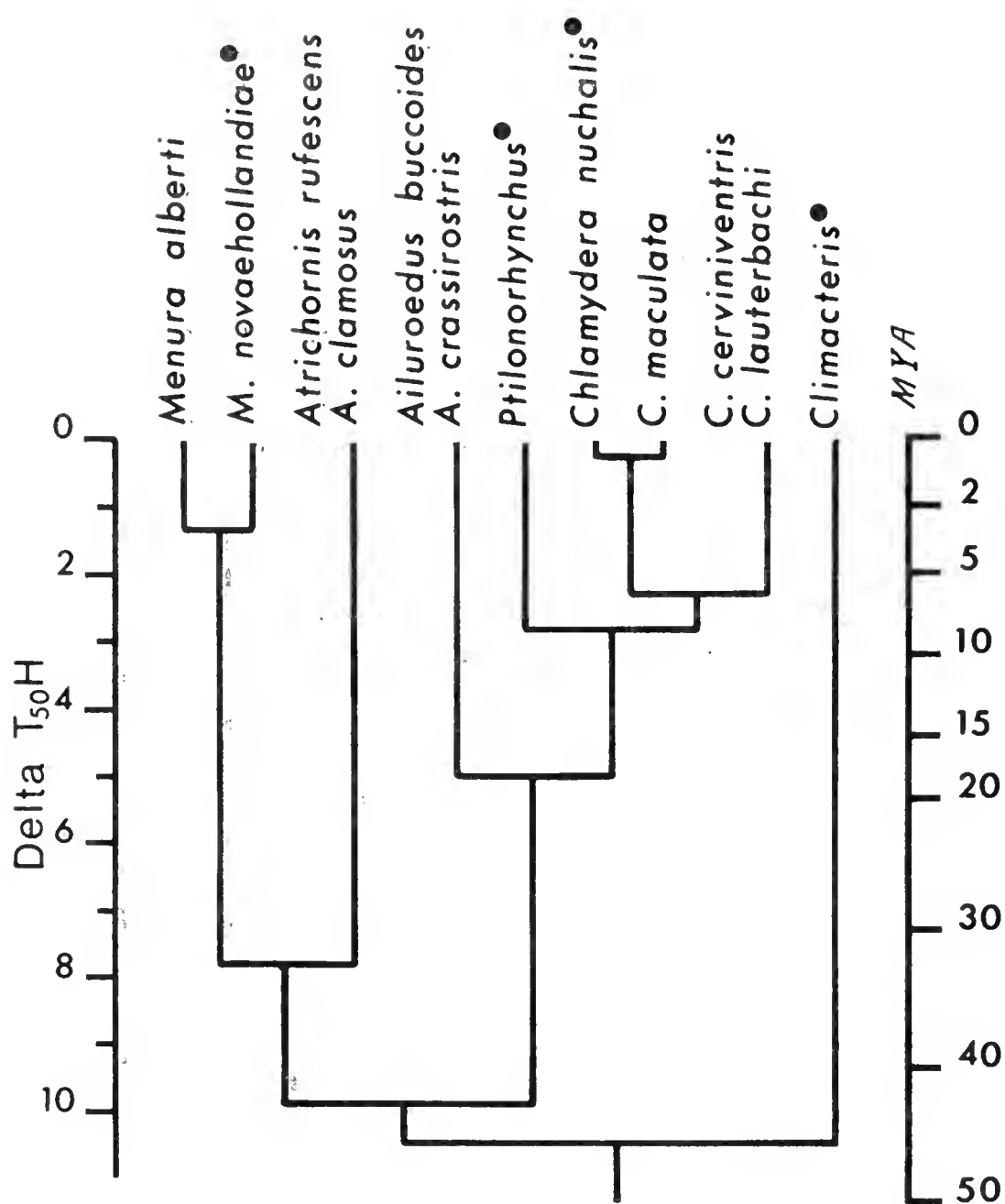


Fig. 4. Superfamily Menuroidea

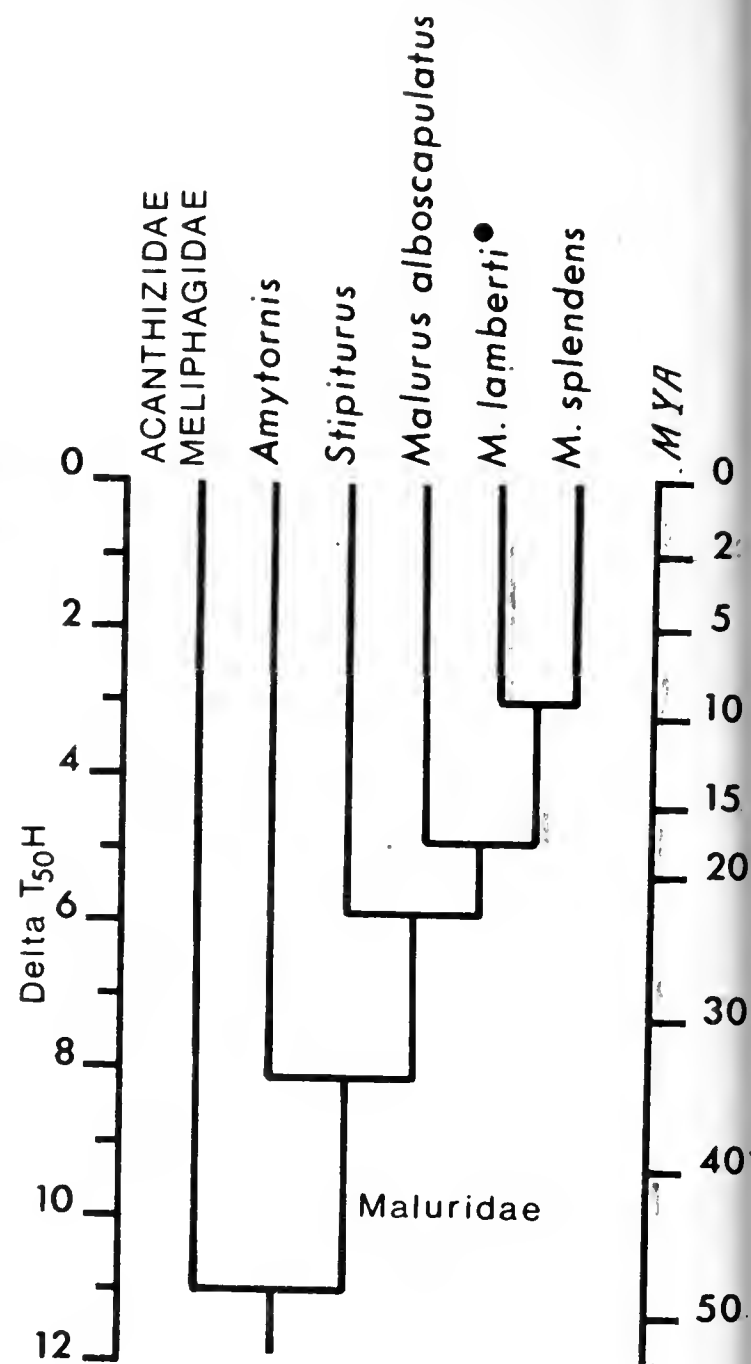


Fig. 5. Family Maluridae

honeyeaters as Anthochaera, Phylidonyris, and Entomyzon than are such unquestionable meliphagids as Certhionyx and Myzomela. Evidence that Ephthianura and Ashbyia are honeyeaters has also been presented by Sibley (1970:73; 1976:566) and Parker (1973).

The Australo-Papuan warblers (Acanthizidae) are not related to the Sylviidae, but are an endemic group that includes the genera Acanthiza, Sericornis, Crateroscelis, Dasyornis, Smicrornis, Gerygone, Aphelocephala, etc. of Schodde (1975).

The pardalotes (Pardalotus) are also members of the Acanthizidae, not relatives of the flowerpeckers (Dicaeum), which are related to the sunbirds (Nectarinia). These relationships were also evident in the electrophoretic patterns of the egg white proteins (Sibley, 1976:567).

The Superfamily Corvoidea includes the other Australo-Papuan "Old Endemics," plus the crows, magpies, jays (Corvini), the orioles and cuckoo-shrikes (Oriolini), the shrikes (Laniinae), the vireos (Vireoninae, Sibley and Ahlquist, 1982c), the fairy-bluebirds (Irena), the ioras (Aegithina), the leafbirds (Chloropsis), the Papuan berrypeckers (Melanocharis), and possibly other Australasian genera.

The first branch in the corvoid phylogeny separated the ancestor of the Papuan robins and flycatchers (Eopsaltriidae) from that of the other groups. The

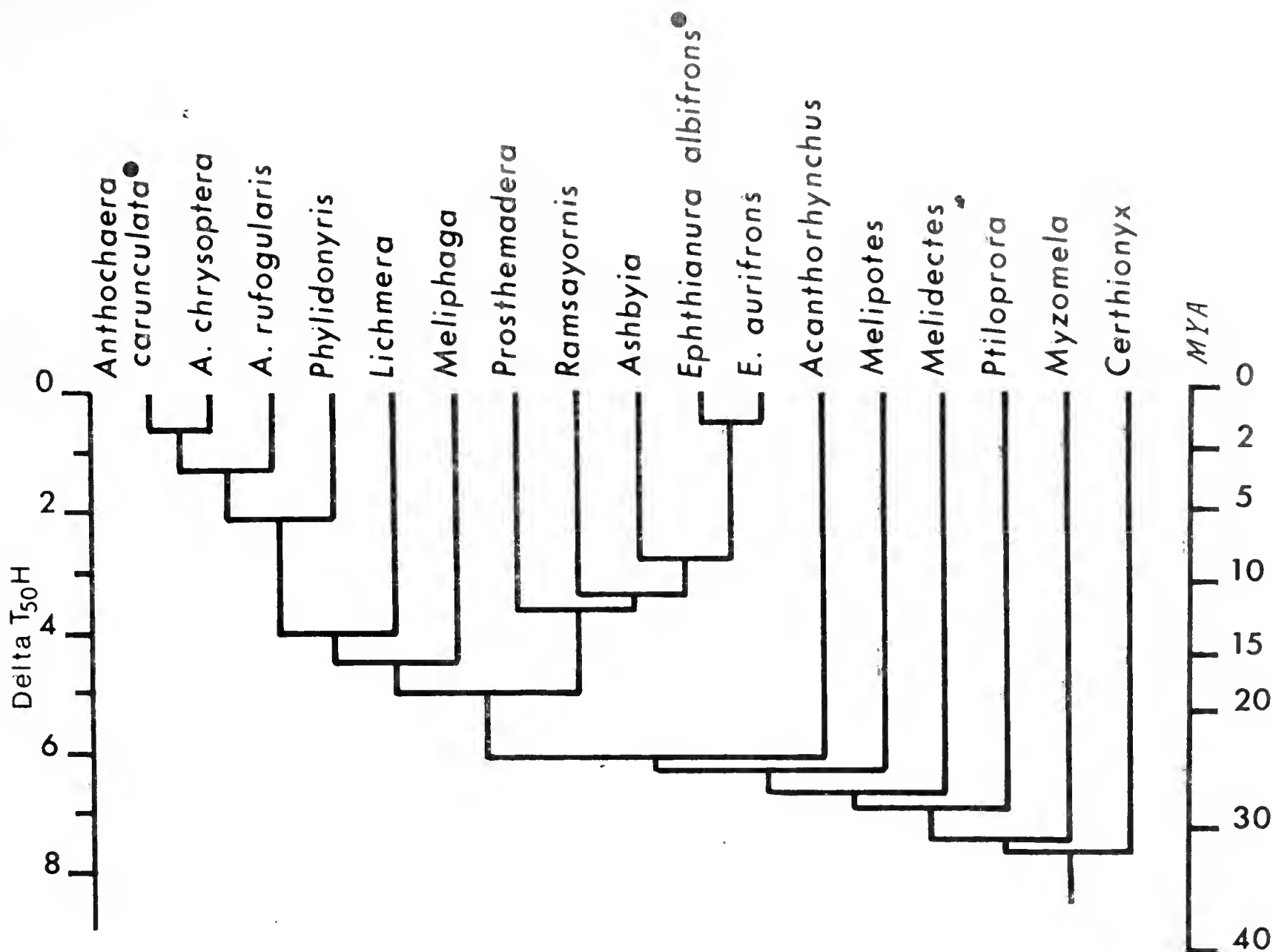


Fig.6. Family Meliphagidae

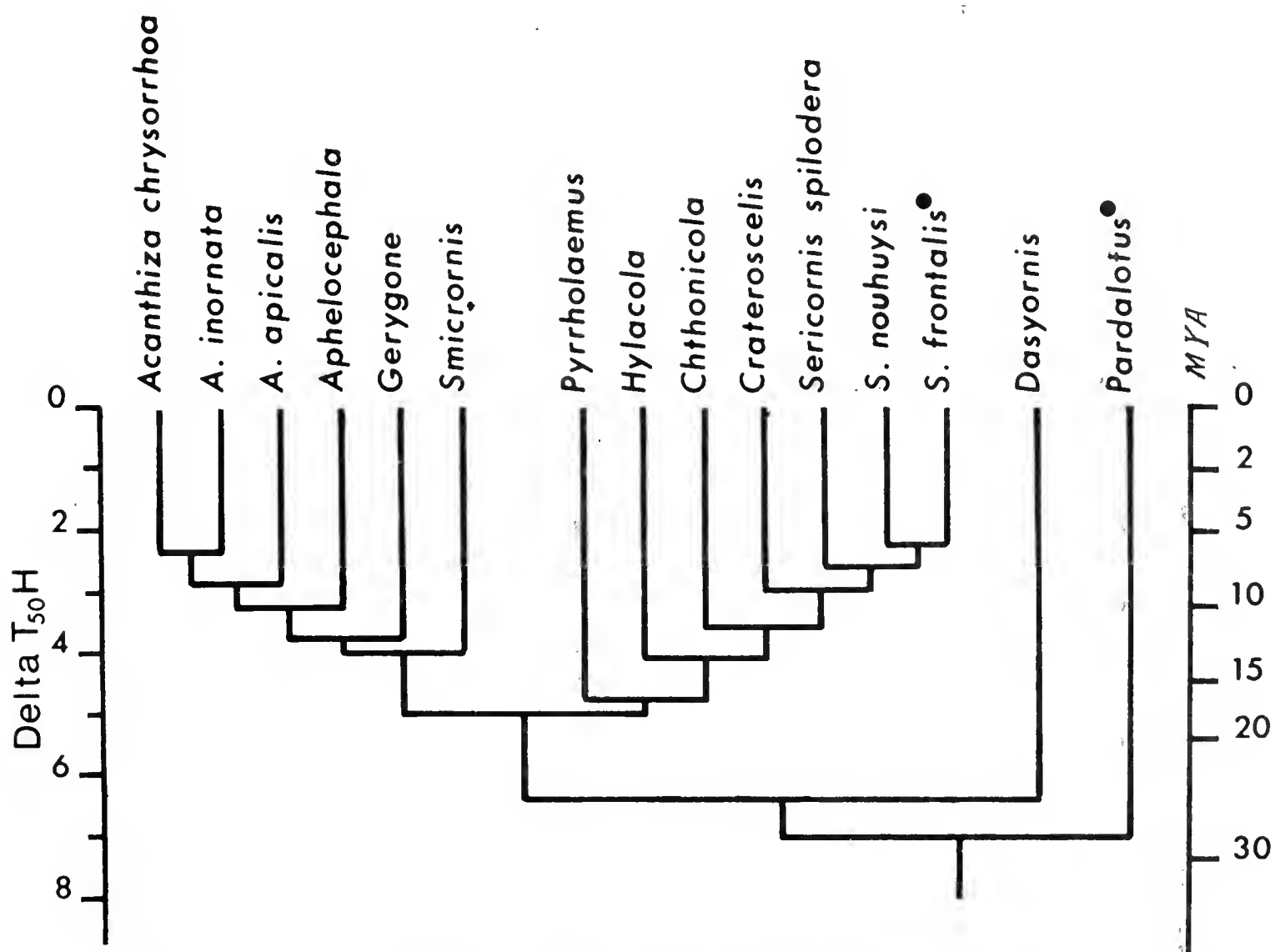


Fig.7. Family Acanthizidae

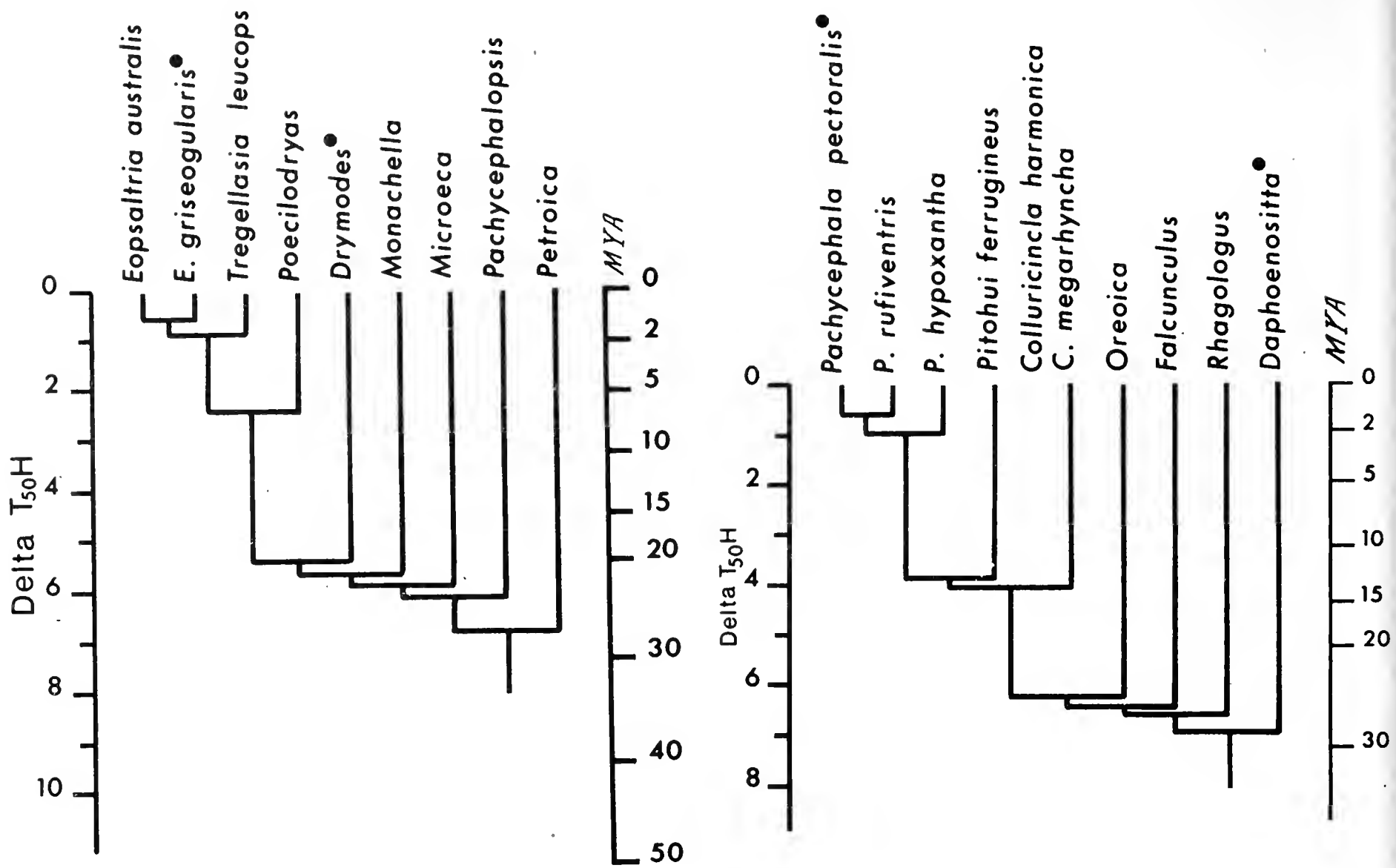


Fig. 8. Family Petroicidae

Fig. 9. Family Corvidae: Subfamily Pachycephalinae

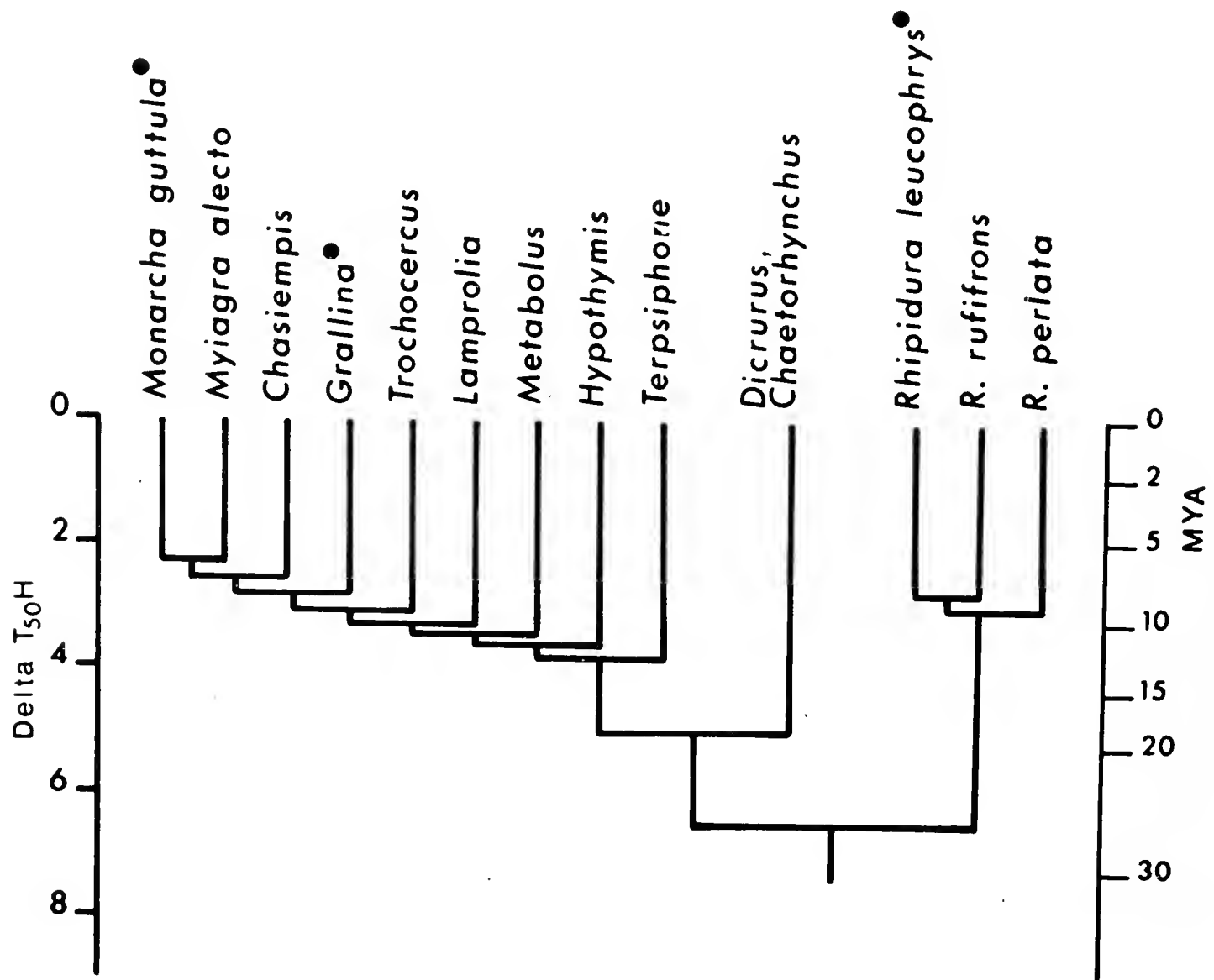


Fig. 10. Family Corvidae: Subfamily Monarchinae

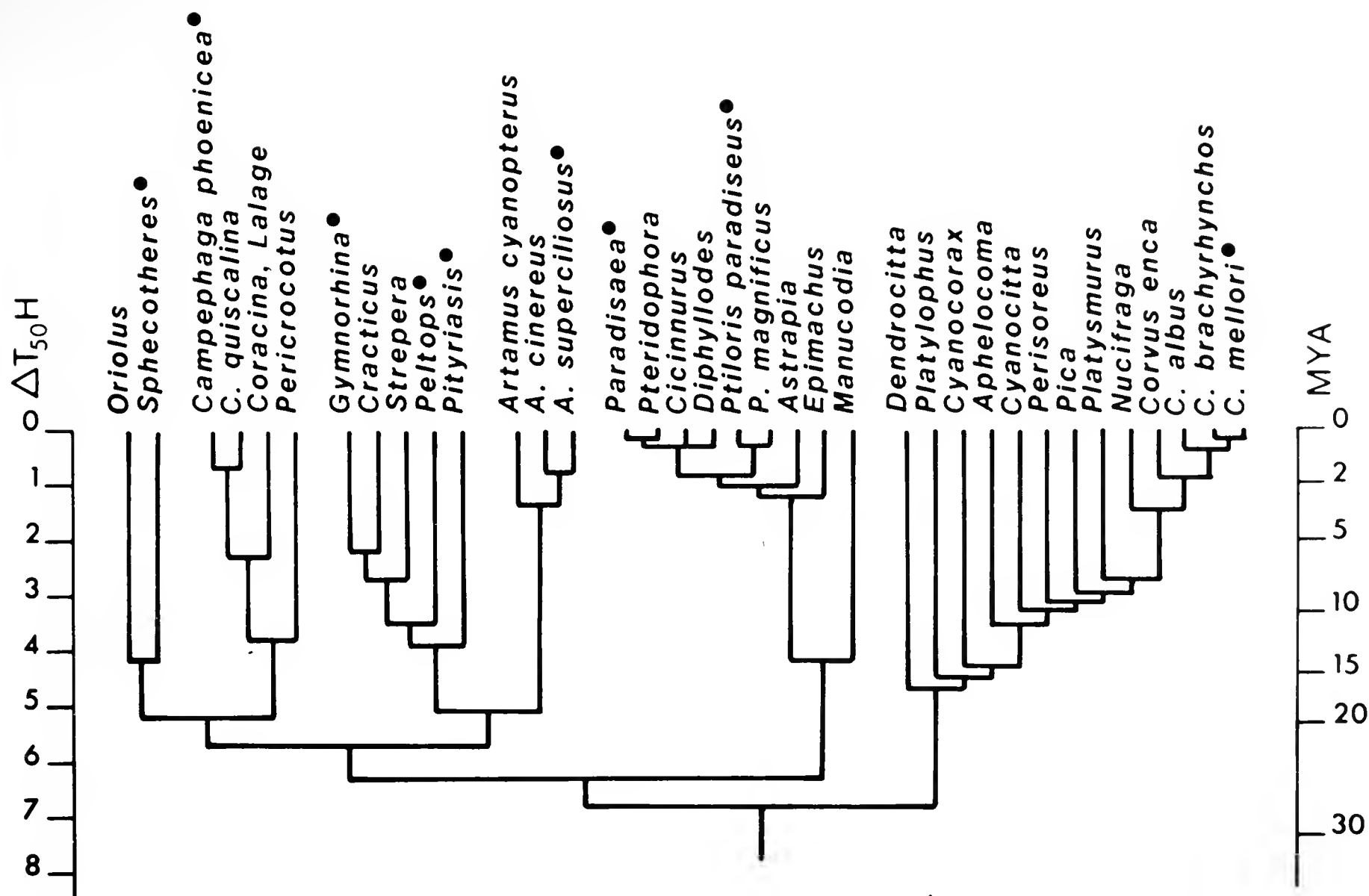


Fig. 11. Family Corvidae: Subfamily Corvinae

scrub-robins (Drymodes), often thought to be turdine thrushes or timaliine babblers, are members of the Eopsaltriidae (Sibley and Ahlquist 1982e). Other genera are Petroica, Eopsaltria, Melanodryas, Microeca, Tregellasia, Poecilodryas, Heteromyias, Monachella, Peneothello, and Pachycephalopsis. These genera are not closely related to the true thrushes (Turdinae), the Old World flycatchers (Muscicapinae) (Sibley and Ahlquist, 1980), or the true babblers.

The genus Orthonyx is so distant from other corvids that we place it in a monotypic family. Similarly, the genus Pomatostomus, often thought to be a timaliine babbler, is also distinct and is given family rank. It is not related to the Sylviidae which includes the true babblers (Timaliini).

The remaining corvids must be included in the family Corvidae if we are to preserve the structure of a cladistic classification. Even so, we are forced to violate the principle of coordinate ranking for sister groups to avoid an excessive number of categorical ranks. To accommodate to this compromise we have used the principles of "subordination and sequencing" proposed by Nelson (1973). The resulting classification reduces several morphologically distinctive groups to subfamilies and tribes but it is a reasonably accurate reflection of the phylogeny. If we were to inflate the ranks so that tribes became families the entire hierarchy would have to shift so much that the groups traditionally recognized as Orders would, in some cases, become Classes. We believe it is preferable to choose the arrangement we have adopted in this paper although it departs more than we would prefer from previous categorical assignments. Our classification is also a step toward the ideal of "categorical equivalence" among all

groups of organisms, which Hennig (1966) advocated and which we have discussed elsewhere (Sibley and Ahlquist, 1982d).

The subfamily Cinclosomatinae includes the Australo-Papuan quail-thrushes (Cinclosoma), the three species of Papuan "rail-babblers" (Ptilorrhoa=Eupetes), and the four species of Australian whipbirds and wedgebills (Psophodes).

The Australian White-winged Chough (Corcorax) and the Apostlebird (Struthidea) are closely related genera which can be separated as the subfamily Corcoracinae. Grallina, often included with these two genera because all three build nests of mud, is actually a large monarch, closely related to Monarcha.

The Pachycephalinae includes the whistlers (Pachycephala), pitohuis (Pitohui), shrike-thrushes (Colluricincla), Crested Bellbird (Oreoica), the shrike-tits (Falcunculus), the Mottled Whistler (Rhagologus), and probably other New Guinea endemics related to these genera.

The nuthatch-like Australo-Papuan sittellas (Daphoenositta) are most closely related to the pachycephalines and were the earliest branch within the group. We assign them to the Tribe Neosittini. The true nuthatches (Sitta) are members of the Superfamily Sylvioidea, Parvorder Muscicapae. (Sibley and Ahlquist, 1982f, g).

The monarch flycatchers (Monarchinae) occur in Australia, New Guinea, many Pacific islands, southern Asia, and Africa. We have DNA hybridization data for Monarcha, Myiagra, Arses, Hypothymis, Philentoma, Metabolus, Terpsiphone, Trochocercus, Lamprolia, and Chasiempis showing that all are monarchs.

The Australo-Papuan magpie-larks (Grallina cyanoleuca and bruijni) are also monarchs. G. cyanoleuca, at an average delta T_{50}^H 3.0 from typical monarchs, is barely a separate genus and is as close to Monarcha as are Lamprolia (3.3), or Terpsiphone (3.7).

The drongos (Dicrurus, Chaetorhynchus) are also monarchines with an average delta T_{50}^H of 5.0 from Monarcha and Grallina. We recognize the Tribe Dicrurini for the drongos.

The fantails (Rhipidura) are the descendants of the earliest branch in the monarchine cluster and are therefore the sister group of all the other monarchs. We recognize a Tribe Rhipidurini and list the fantails first in the Monarchinae in accordance with the principles of subordination and sequencing.

The other corvoids are placed in the subfamily Corvinae which thus includes at least six groups traditionally ranked as families, namely, the Corvidae, Paradisaeidae, Artamidae, Cracticidae, Oriolidae, and Campephagidae. That these groups should be so closely related is surprising but their most recent common ancestors began to diverge ca. 25-30 mya in the Oligocene as indicated by the average delta T_{50}^H of 6.8 for the branch between the Corvini and the other groups in Fig. 3.

The Tribe Corvini contains the same taxa as the traditional Corvidae, namely, the crows, magpies, and jays.

The Paradisaeini includes only the birds-of-paradise. The sexually monomorphic manucodes (Manucodia) branched from the dimorphic taxa ca. 13-15 mya and the dimorphic taxa are closely related to one another. From Ptiloris paradiseus we obtained delta T_{50}^H values, as follows: Ptiloris magnificus 0.3; Pteridophora alberti 0.8; Paradisaea minor 0.9; Astrapia mayeri 1.0; Epimachus meyeri 1.1; Cicinnurus regius 1.3; Diphyllodes

magnificus 1.4. These values indicate that these taxa have diverged from one another within the past 3 my. All could be contained in a single genus and it is not surprising that at least ten of the sexually dimorphic genera have hybridized and produced viable offspring (Mayr, 1942:260). The distinctive male plumages and displays evolved in response to sexual selection and selection against hybridization and are thus additional evidence of their close relationships, not of genetic diversity (Sibley, 1957). Diamond (1972) proposed that the 20 genera of birds-of-paradise usually recognized could be reduced to 10.

The Cracticini includes the woodswallows (Artamus), the Australo-Papuan currawongs (Strepera), magpies (Gymnorhina), and butcherbirds (Cracticus), and the Bornean Bristlehead (Pityriasis gymnocephala). Artamus branched from the lineage leading to the other genera ca. 18-20 mya and the Artamidae have been recognized as a monotypic family in all recent classification. Pityriasis was placed with Cracticus and Gymnorhina from its discovery in 1835 until recent years when some authors placed it in the "Prionopidae." It is closest to Cracticus at ΔT_{50}^H 3.9 (Ahlquist et al., in press). The Papuan genus Peltops is also a cracticine, most closely related to Pityriasis.

The Oriolini includes the Old World orioles ("Oriolidae") and the cuckoo-shrikes ("Campephagidae"). It was another surprise to discover that these two morphologically distinctive groups are so closely related. They diverged from one another ca. 15-20 mya and from the Cracticini ca. 20-22 mya.

The DNA hybridization data, and the geological history of the southern continents, suggest that the Corvi originated and radiated in Australia during the Tertiary, when Australia was isolated from Africa, Asia, and South America. In the later Tertiary, when Australia had drifted closer to Asia, several corvoid taxa emigrated and produced new radiations in Eurasia and Africa. A few corvoids reached the New World, and several have recently re-entered Australia, for example Corvus, Dicrurus, and Oriolus.

The Parvorder Muscicapae

The remaining oscines are members of the Parvorder Muscicapae, which we subdivide into three superfamilies, Turdoidea, Sylvioidea, and Fringilloidea. See Figures 12-20.

The Turdoidea includes the Bombycillidae, Cinclidae, Sturnidae, and Turdidae. See Figures 13 and 14. The waxwings (Bombycilla), silky flycatchers (Phainopepla, Phainoptila, Ptilogonys), and the Palm Chat (Dulus) were studied by Arvey (1951) who concluded that they were closely related and should be included in a single family. Sibley (1973) noted similarities between the electrophoretic patterns of the egg white proteins of Phainopepla and the thrush genus Myadestes and suggested that the silky flycatchers "are more closely related to Myadestes than to any other genus...." The DNA data also show that the silky flycatchers (and other bombycillids) are related to the thrushes but that they are not more closely related to Myadestes than to other turdine genera.

The dippers (Cinclus) have usually been thought to be allied to the wrens or to the thrushes. The egg white protein evidence (Sibley 1970:66) supported a dipper-thrush alliance and the DNA data confirm this relationship. The Cinclidae branched from the turdine lineage in the Eocene, ca. 40-45 mya.

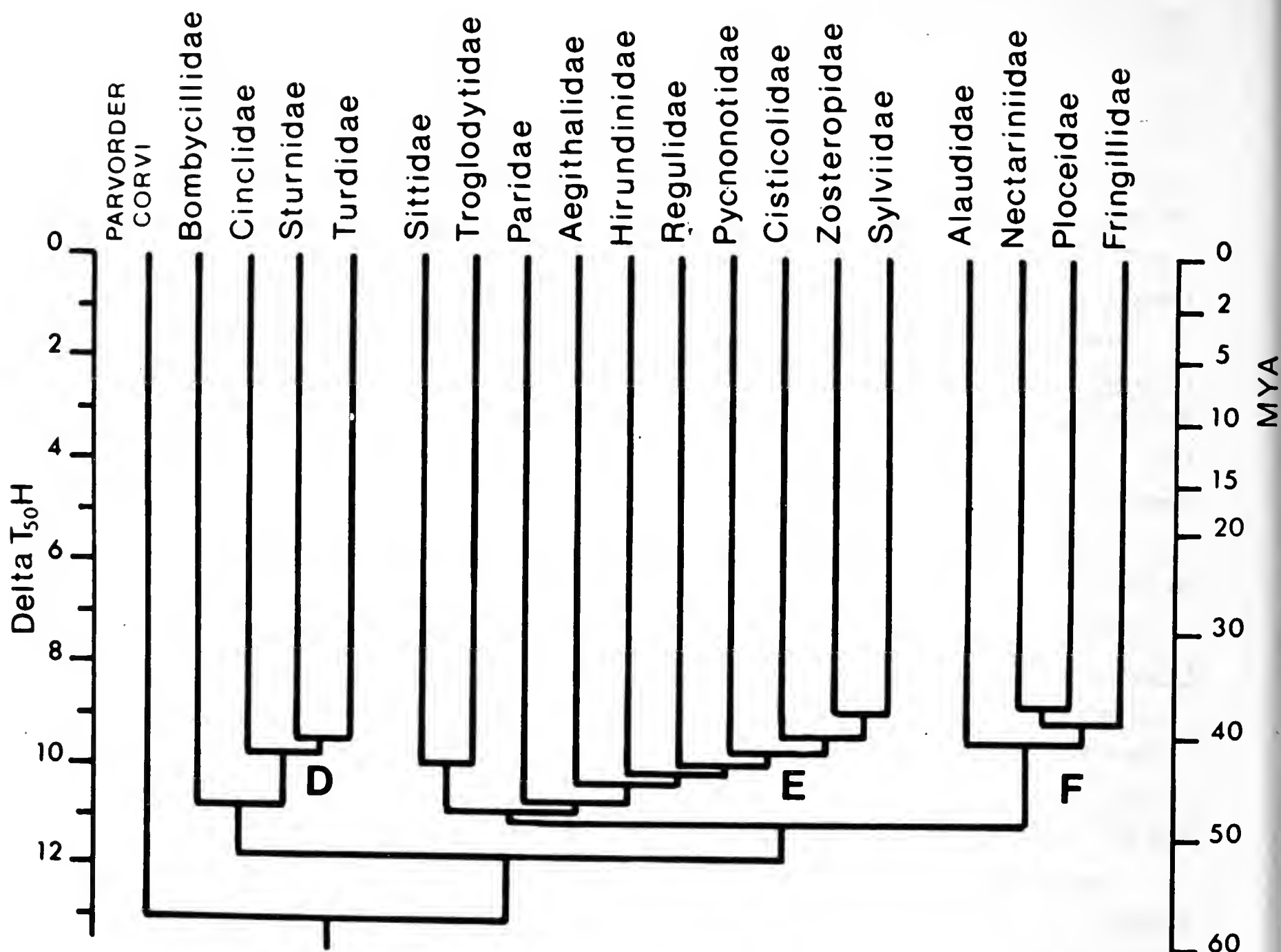


Fig.12. Families of the Parvorder Muscicapae. Group D=Turdoidea, E=Sylvioidea, F=Fringilloidea

The Turdidae includes the typical thrushes (Turdinae) and the Old World flycatchers and chats (Muscicapinae). These two subfamilies diverged ca. 38-40 mya. Figure 14 depicts some of the phylogeny of the Turdidae.

The DNAs of 23 of the 62 species of Turdus were compared with the radio-labeled DNA of T. migratorius. The delta $T_{50}H$ values ranged from 0.2 (T. plumbeus) and 0.6 (T. fulviventris) to 3.4 (T. fuscater). Myadestes, at 7.2 from Turdus, and Monticola at 8.2 from both Turdus and Myadestes, could be recognized as additional subfamilies. They demonstrate the diversity and long history of the true thrushes.

Chlamydochaera jefferyi is a Bornean endemic that had been placed in the "Campephagidae" by all authors until Ames (1975) found syringeal similarities to the turdines and suggested that Chlamydochaera is actually a thrush. We have confirmed Ames' proposal by a DNA hybridization study which shows that Chlamydochaera is closely related to Turdus at delta $T_{50}H$ 4.2 (Ahlquist et al.).

The Muscicapinae provide an instructive example of ecological specializations and correlated morphological adaptations. The Old World flycatchers (Muscicapini) have usually been thought to be closely related to the monarchs (Monarchinae:Corvidae) and whistlers (Pachycephalinae:Corvidae), and the chats (Erithacini) have always been

placed with the turdine thrushes. The DNA data show that the muscicapines and erithacines are sister groups that diverged from a common ancestor ca. 28 mya and evolved their morphological differences as they adapted to different ecological niches. Because their next nearest relatives are the turdine thrushes, it seems likely that the common ancestor of the living turdids was thrush-like and that the muscicapines converged on the monarchs and whistlers as they adapted to the flycatcher niche.

Sibley and Ahlquist (1980) showed that the "Muscicapidae" of Hartert (1910), and many subsequent authors, is not tenable because it is a polyphyletic taxon. It included members of both of the parvorders, and of four of the six superfamilies, we recognize in the suborder Passeres.

The starlings (Sturnus, etc.) have usually been thought to be related to the crows, orioles, drongos, weaverbirds, or troupials, and the mockingbirds (Mimus, Toxostoma, etc.) have been placed near the thrushes and/or the wrens. Thus it was a surprise to discover that DNA-DNA comparisons indicated that the two groups are actually closely related to one another (Sibley and Ahlquist 1980). A more extensive study has confirmed our earlier conclusion and shown that the starlings and mockingbirds, at $\Delta T_{50}H$ 5.7 from one another, are sister tribes in the family Sturnidae. Their next nearest relatives are the Turdidae (Sibley and Ahlquist, in press a). See Fig. 13.

The Superfamily Sylvioidea includes the nuthatches and wallcreepers (Sittidae), the creepers (Certhia), wrens and gnatcatchers (Troglodytidae), the titmice (Paridae), the long-tailed tits (Aegithalidae), the swallows (Hirundinidae), the kinglets (Regulidae), the bulbuls (Pycnonotidae), the white-eyes (Zosteropidae), and the Old World warblers and babblers (Sylviidae). See Figures, 12, 13, 15 and 16.

The nuthatches (Sitta) and the wallcreepers (Tichodroma) are sister taxa ($\Delta 8.9$) and they shared a common ancestor with the other sylvioids ca. 40-45 mya (10.0). Löhr (1964) also concluded that Sitta and Tichodroma are related more closely to one another than to Certhia. The Sittidae are not related to the Australo-Papuan sittellas (Daphoenositta), which are members of the corvid subfamily Pachycephalinae (Sibley and Ahlquist, 1982f), nor to the Australo-Papuan treecreepers (Climacteris) which are members of the Menuroidea (Figs. 2,3). It also seems unlikely that the Sittidae are closely related to the vangid Coral-billed Nuthatch (Hypositta) of Madagascar, to the Afro-Indian Spotted Creeper (Salpornis), or to the Philippine creepers (Rhabdornis). We lack DNAs of these three genera and their relationships are uncertain.

The Troglodytidae consists of the Northern creepers (Certhiinae), the wrens (Troglodytinae), and the Polioptilinae, which includes the Verdin (Auriparus), the gnatwrens (Microbates, Ramphocaenus), and the gnatcatchers (Polioptila). The subfamily Certhiinae branched from the others at $\Delta 8.5$, ca. 35-40 mya, and the Troglodytinae and Polioptilinae diverged ca. 30-35 mya (7.9). See Figs. 13 and 16.

The Troglodytinae and Polioptilinae obviously originated in the New World. Rand and Traylor (1953) proposed that the Neotropical genera Microbates and Ramphocaenus are related to Macrosphenus of Africa, rather than to Polioptila. It seems clear that convergent morphological characters, not close relationship, accounted for this proposal.

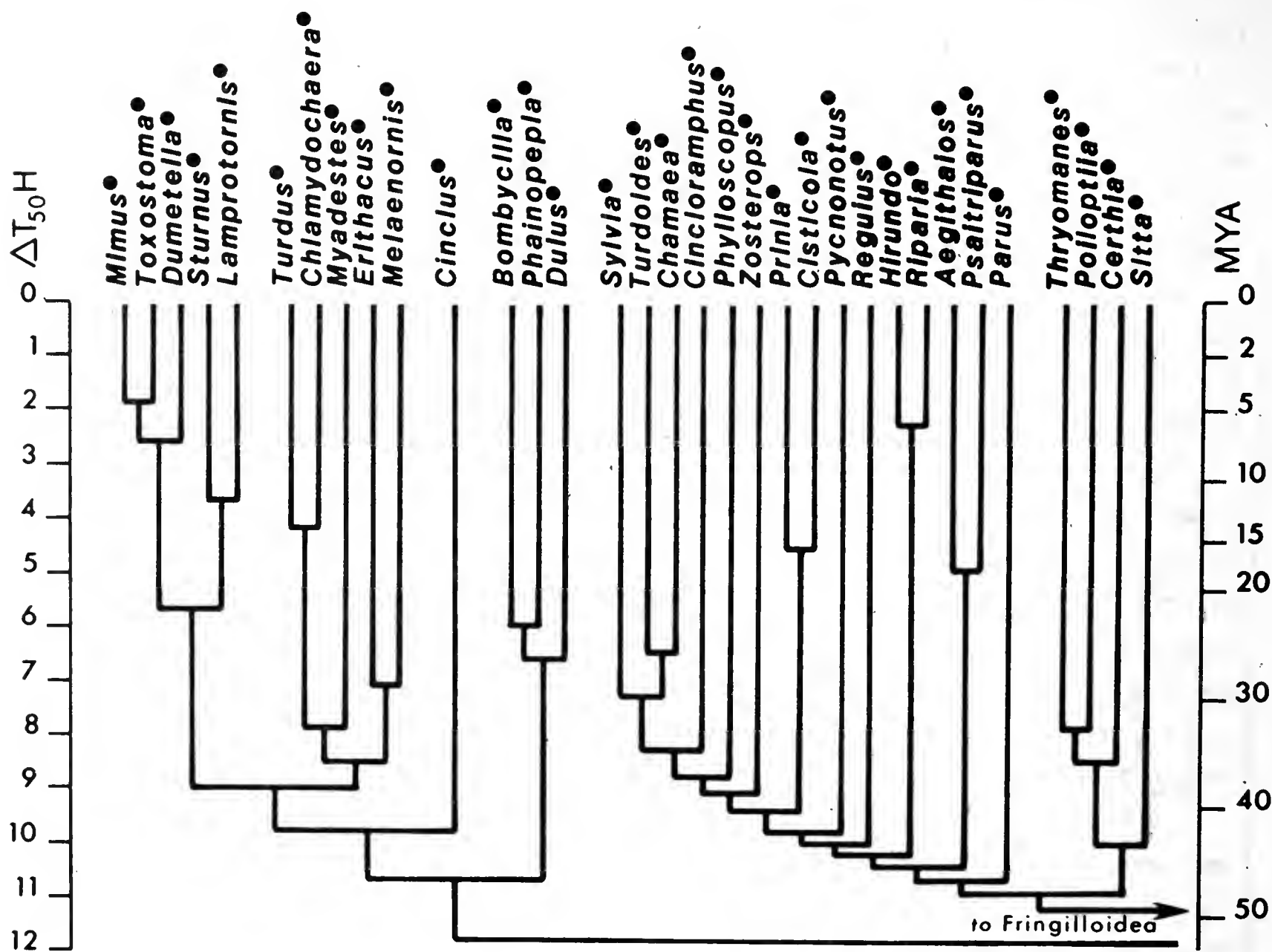


Fig.13. Superfamilies Turdoidea and Sylvioidea

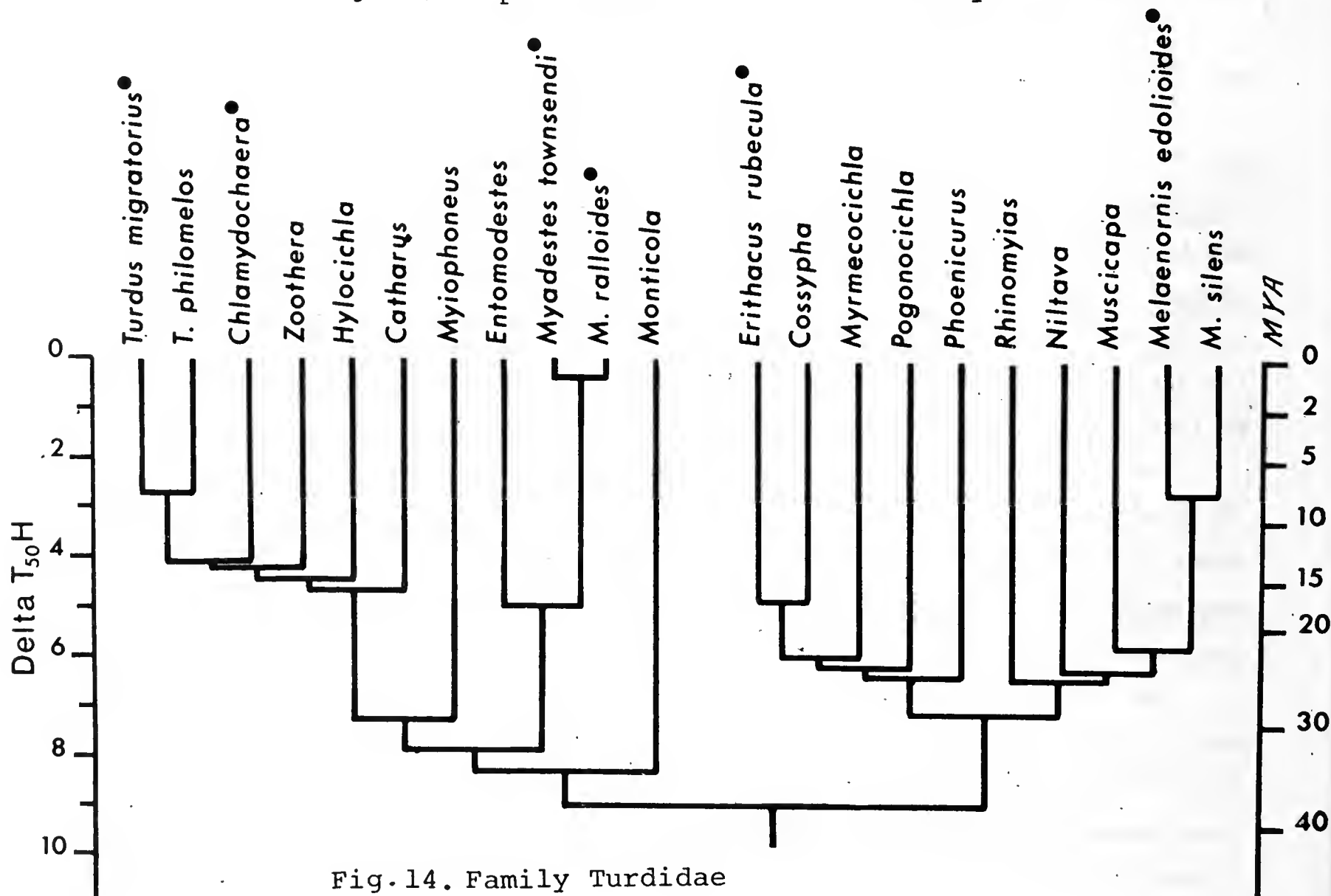


Fig.14. Family Turdidae

A similar example concerns the relationships of the Verdin (Auriparus flaviceps) of the southwestern United States and northern Mexico. Auriparus usually has been placed near Remiz and Anthoscopus in the Remizidae (e.g. Snow 1967) or in the Paridae. The DNA data reveal that Auriparus is a member of the Polioptilinae at $\Delta 5.1$ from Polioptila and that African Anthoscopus and, presumably, Eurasian Remiz, are parids. We lack the DNA of Remiz.

The Paridae includes the penduline tits (Anthoscopus, Remiz) and the titmice and chickadees (Parus). The Remizinae branched from the Parinae ca. 35-40 mya ($\Delta 8.6$) and the Paridae diverged from the other sylvioids ca. 45-50 mya.

The Aegithalidae, including Eurasian Aegithalos and western North American Psaltiriparus, diverged from other sylvioids ca. 45-50 mya, and from one another ca. 15-20 mya, in the Miocene. The ancestor of the bushtits may have entered North America via the Bering land bridge.

The swallows (Hirundinidae) have been viewed as distinct from all other oscines because of the unique structures of the syrinx and the tarsi. The muscicapine flycatchers have been most frequently suggested as possible relatives but the Hirundinidae have been placed at or near the beginning of the sequence of oscine taxa in most classifications. The DNA hybridization evidence shows that they are the living descendants of a lineage that branched from other sylvioid groups ca. 45 mya. Their specialized syringes and tarsi are clearly derived characters which evolved after the swallows diverged from the last common ancestor they shared with other sylvioids (Sibley and Ahlquist 1982i).

The kinglets (Regulus) usually have been placed with or near the sylviine warblers but they are distinctive in many ways and their affinities have been uncertain. The reason for the uncertainty is now clear because the DNA data reveal Regulus to be the descendant of a remarkably ancient branch of the sylvioid tree. Although the living species of Regulus are closely related to one another, they last shared a common ancestor with other living sylvioids ca. 40-45 mya (See Fig. 15). We therefore recognize the family Regulidae.

The bulbuls (Pycnonotidae) are usually given family rank but thought to be allied to the cuckoo-shrikes (Campephaga, etc.), the fairy bluebirds (Irena), and the leafbirds (Aegithina, Chloropsis). The DNA comparisons show that the bulbuls, including the shrike-like genus Nicator, are sylvioids, not members of the Corvi (see Figs. 12, 13 and 15). Virtually all classifications have accorded the white-eyes family rank as the Zosteropidae, but their affinities have been obscure. Sibley (1970:84-85) reviewed their taxonomic history which shows that the brush-tipped tongue has been the basis for placing the white-eyes near the sunbirds, flowerpeckers, and honeyeaters. Beecher (1953) interpreted his jaw muscle data as evidence that Zosterops was derived from the bulbuls and related to the sunbirds and flowerpeckers. These various opinions demonstrate once again the difficulties encountered in trying to use convergence-prone morphological structures as clues to phylogeny.

The DNA data show that the Zosteropidae are sylvioids (Figs. 13, 15) and that they branched from the other sylvioid lineages ca. 38-40 mya. It is of interest to note that "Rukia" oleaginea of Yap, Caroline Islands, is only $\Delta 1.5$ from

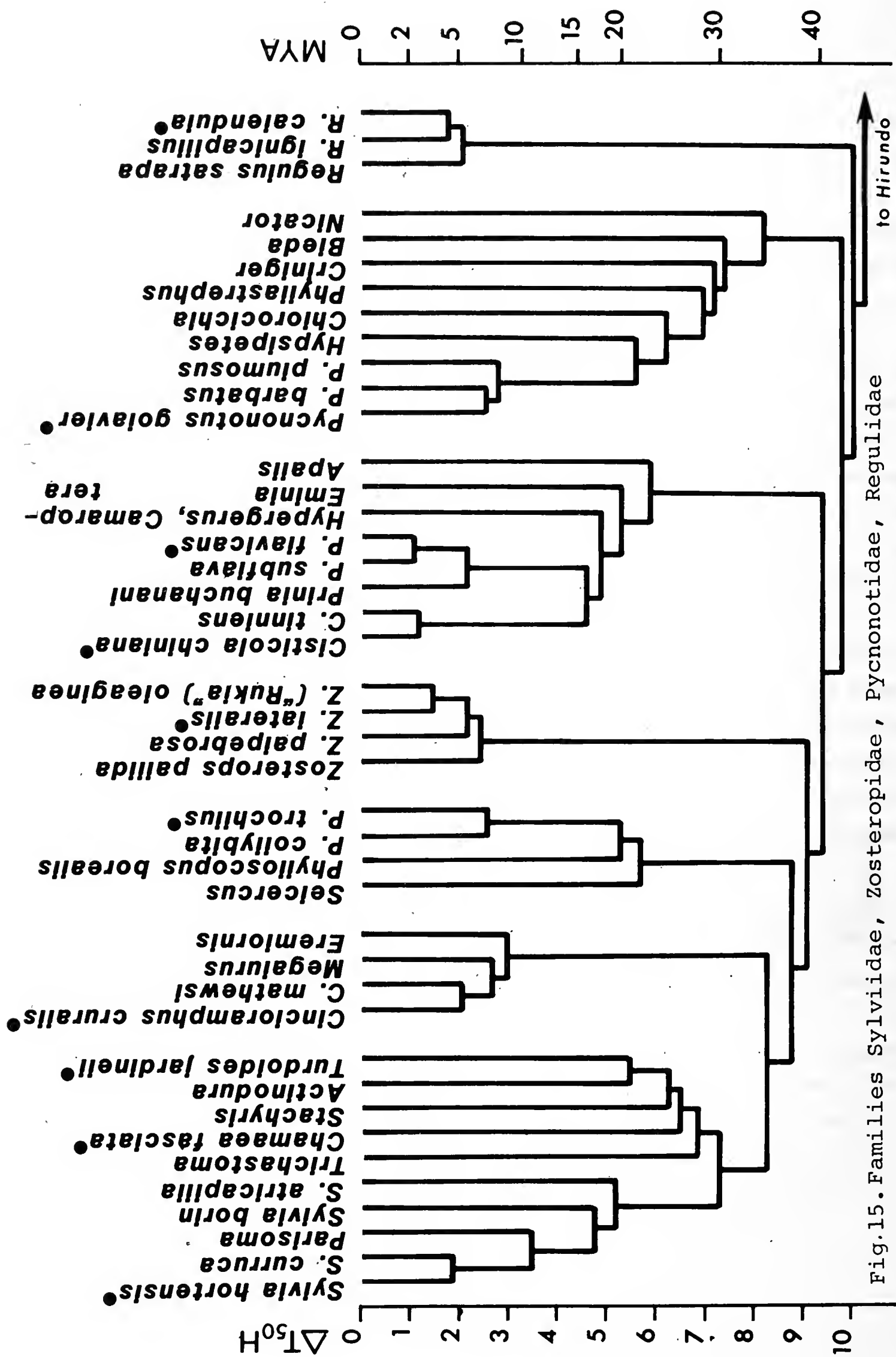


Fig.15. Families Sylvidae, Zosteropidae, Pycnonotidae, Regulidae

Zosterops lateralis of Australia, while Z. pallida of South Africa is $\Delta 2.4$ from Z. lateralis. We suggest that Rukia be included in Zosterops.

The relationships of the many genera of "Old World warblers" to one another and to other groups of small, ten-primaried oscines have been discussed and debated for more than a century without producing a convincing taxonomic treatment. Sibley (1970:68-74) reviewed the literature and Sibley and Ahlquist (1980; 1982 b,h) have presented DNA hybridization data for some aspects of these problems. The following statements summarize our present understanding of the Sylviidae.

1. The Maluridae and Acanthizidae are members of the Parvorder Corvi and are not sylviids.

2. The only sylviid genera in Australia are Acrocephalus, Cisticola, Eremiornis, Megalurus, and Cincloramphus, as correctly indicated by Schodde (1975).

3. The only sylviids that occur regularly in the New World are the Arctic Warbler (Phylloscopus borealis kennicotti) which breeds in western Alaska, and the Wrentit (Chamaea fasciata) which is a timaliine babbler (Sibley and Ahlquist 1982b).

4. The babblers (Timaliini) are closely related to Sylvia.

5. The genus Phylloscopus is more distant from Sylvia than Sylvia is from the babblers.

6. Parisoma of Africa is closely related to Sylvia at $\Delta 3.5$.

7. Seicercus of southern Asia is related to Phylloscopus at $\Delta 5.7$.

8. Cisticola, Prinia, Hypergerus, Apalis, Camaroptera, and Eminia are closely related to one another, but are $\Delta 9.0-9.5$ from Sylvia, Phylloscopus, Seicercus, Sphenoeacus, Bradypterus, Chloropeta, Sylvietta, Parisoma, Acrocephalus, Megalurus, and Eremiornis. Thus the Cisticola group apparently branched from the sylvioid stem earlier than did the Zosteropidae. Although our data are incomplete we tentatively recognize the family Cisticolidae (see Figs. 12 and 15).

We conclude that the relationships of many actual or presumed sylviid genera remain uncertain. To solve these questions requires the DNAs of several missing taxa and comparisons of all sylviid genera with additional radio-labeled taxa. Figs. 15 and 16 reflect our present knowledge of the Sylviidae.

We divide the Sylviidae into three subfamilies: Phylloscopinae for the leaf warblers and their allies; Megalurinae for the grass warblers (incl. Cincloramphus, Megalurus, Eremiornis); and Sylviinae for the babblers (Timaliini) and the Old World warblers (Sylviini), including Sylvia and its close relatives.

The Superfamily Fringilloidea is composed of four families; Alaudidae, Nectariniidae, Ploceidae, and Fringillidae. Wetmore (1960) divided the same taxa into 14 families and Wolters (1975-1982) used 23 families. Figures 17-20 present the phylogeny of the Fringilloidea.

The ancestral fringilloid branched from the other oscines ca. 45-50 mya. The living taxa of fringilloids began their divergences ca. 40-45 mya, in the Eocene, when the branch that produced the larks (Alaudidae) diverged ($\Delta 9.5$) from the ploceid-fringillid lineage.

The larks have always been viewed as distinct from all other oscines because

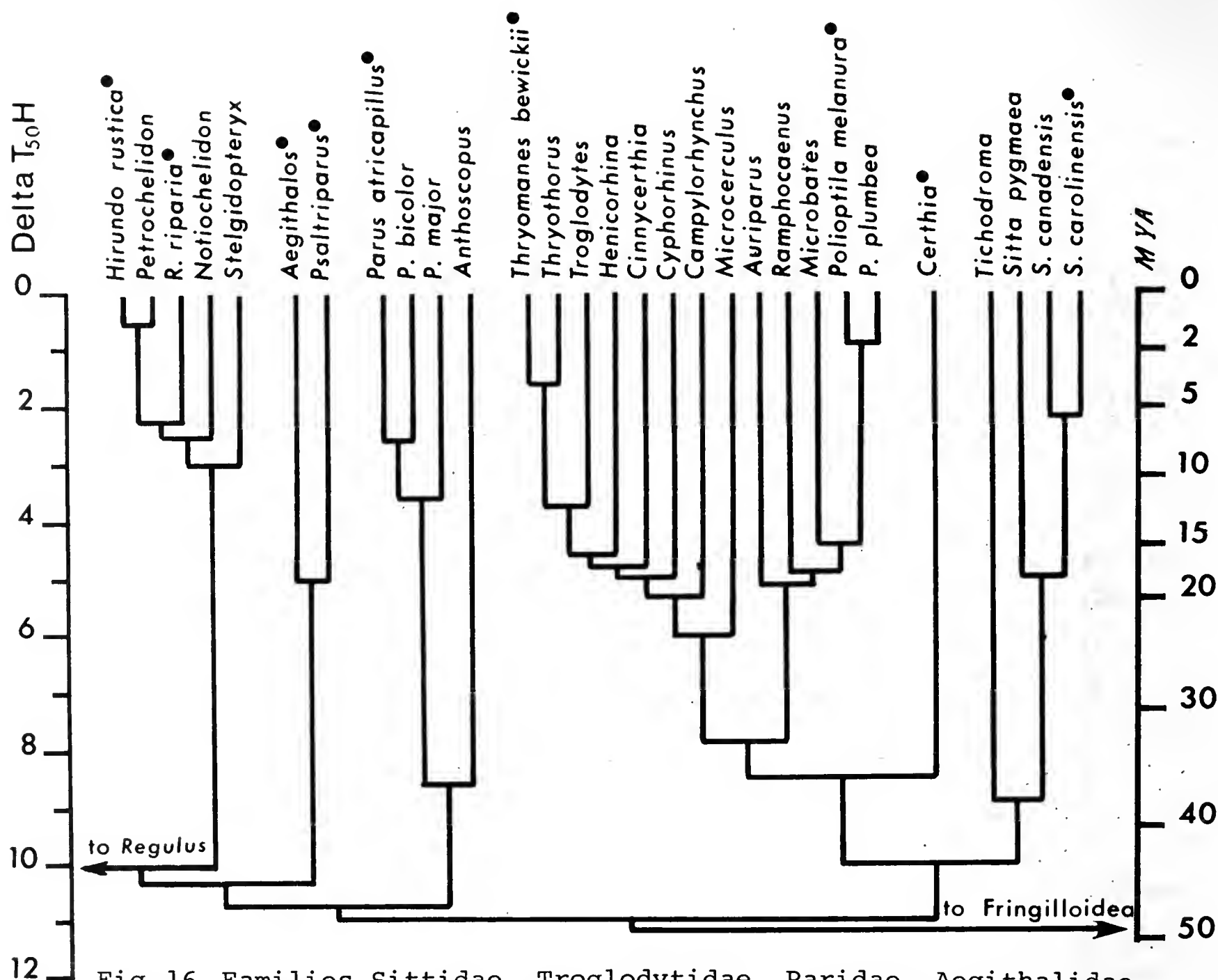


Fig. 16. Families Sittidae, Troglodytidae, Paridae, Aegithalidae and Hirundinidae

they lack an ossified pessulus in the syrinx and have a reticulate pattern of posterior tarsal scutes. These characters define the Alaudidae but they are derived conditions that evolved after the larks diverged from the common ancestor they shared with the other fringilloids.

The Nectariniidae includes the south African sugarbirds (Promeropinae) and the sunbirds and flowerpeckers (Nectariniinae).

Sibley and Ahlquist (1974) proposed that the sugarbirds (Promerops) are related to the starlings on the basis of the electrophoretic patterns of the egg white proteins, but the DNA comparisons prove this to have been an error and show that the Promeropinae is the sister group of the Nectariniinae (Fig. 19).

It is clear that the flowerpeckers are closely related to the sunbirds, and that they are not related to the Australian pardalotes (Pardalotus), which are members of the Acanthizidae in the Parvorder Corvi.

The Ploceidae includes the weaverbirds (Ploceinae), the waxbills (Estrildinae), the sparrows (Passerinae), and two groups not previously recognized as ploceids, the wagtails and pipits (Motacillinae) and the accentors (Prunellinae) (Sibley and Ahlquist, 1981 b,c).

The oldest branch in the ploceid cluster occurred ca. 30-35 mya when the last

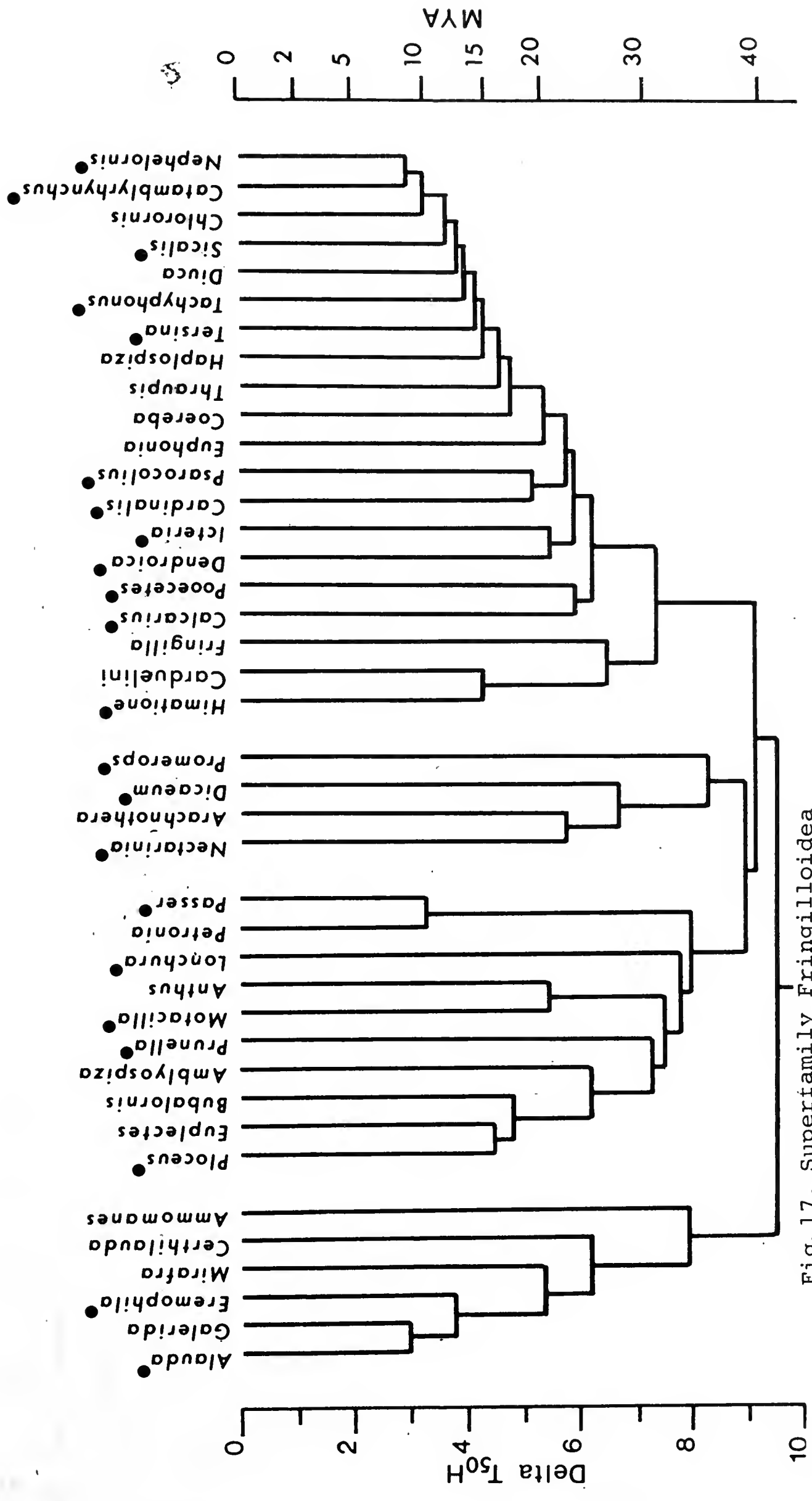


Fig. 17. Superfamily Fringilloidea

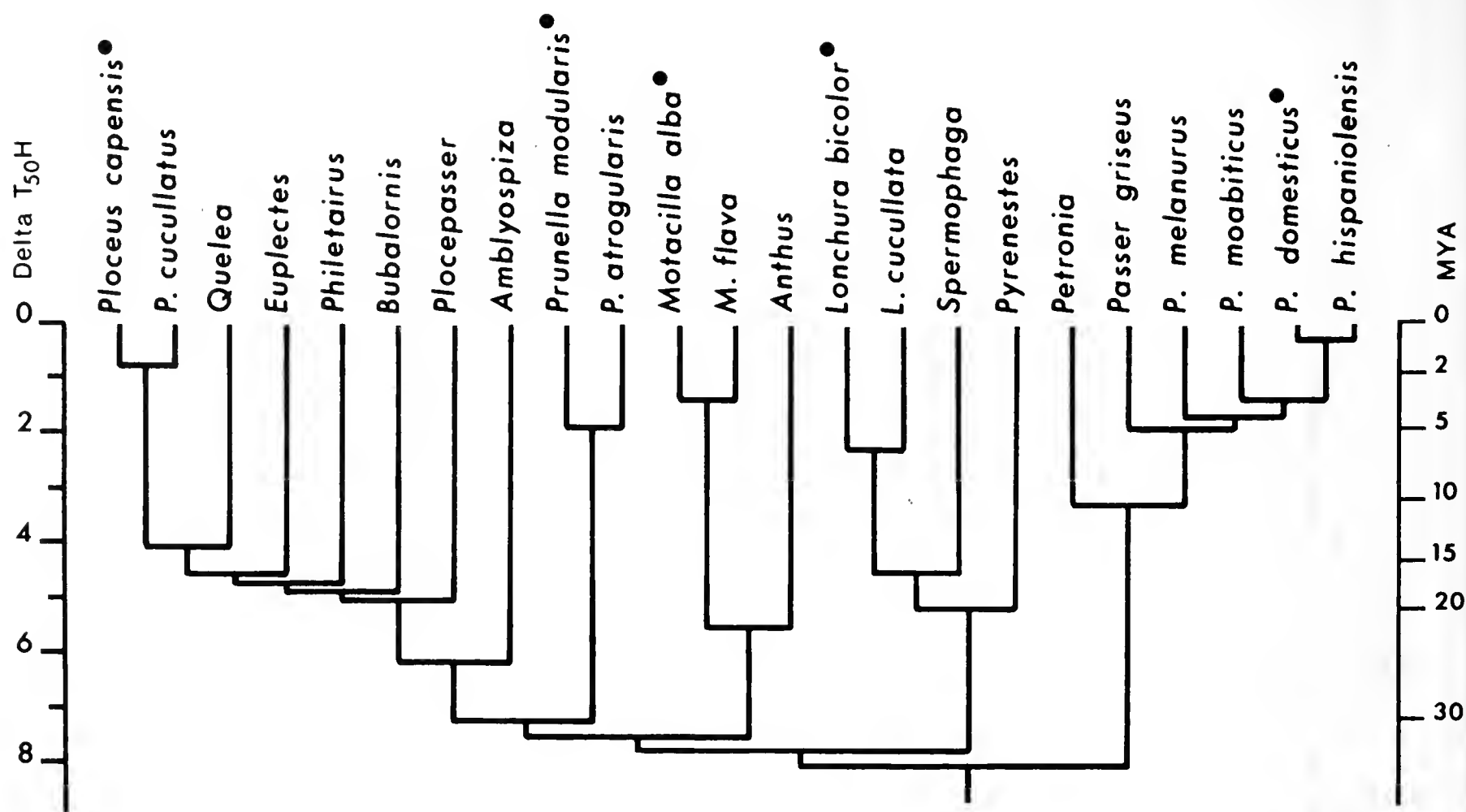


Fig.18. Family Ploceidae

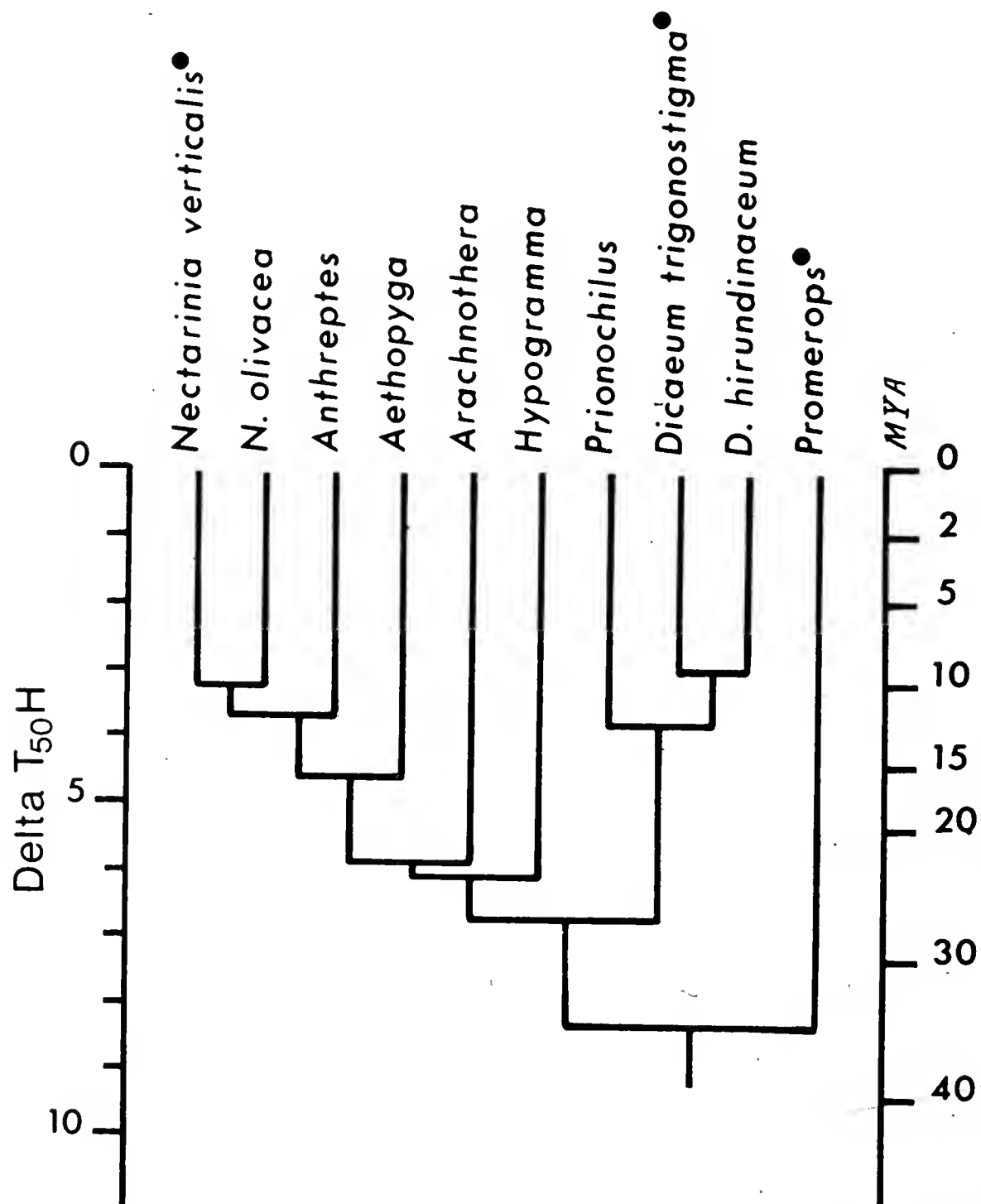


Fig.19. Family Nectariniidae

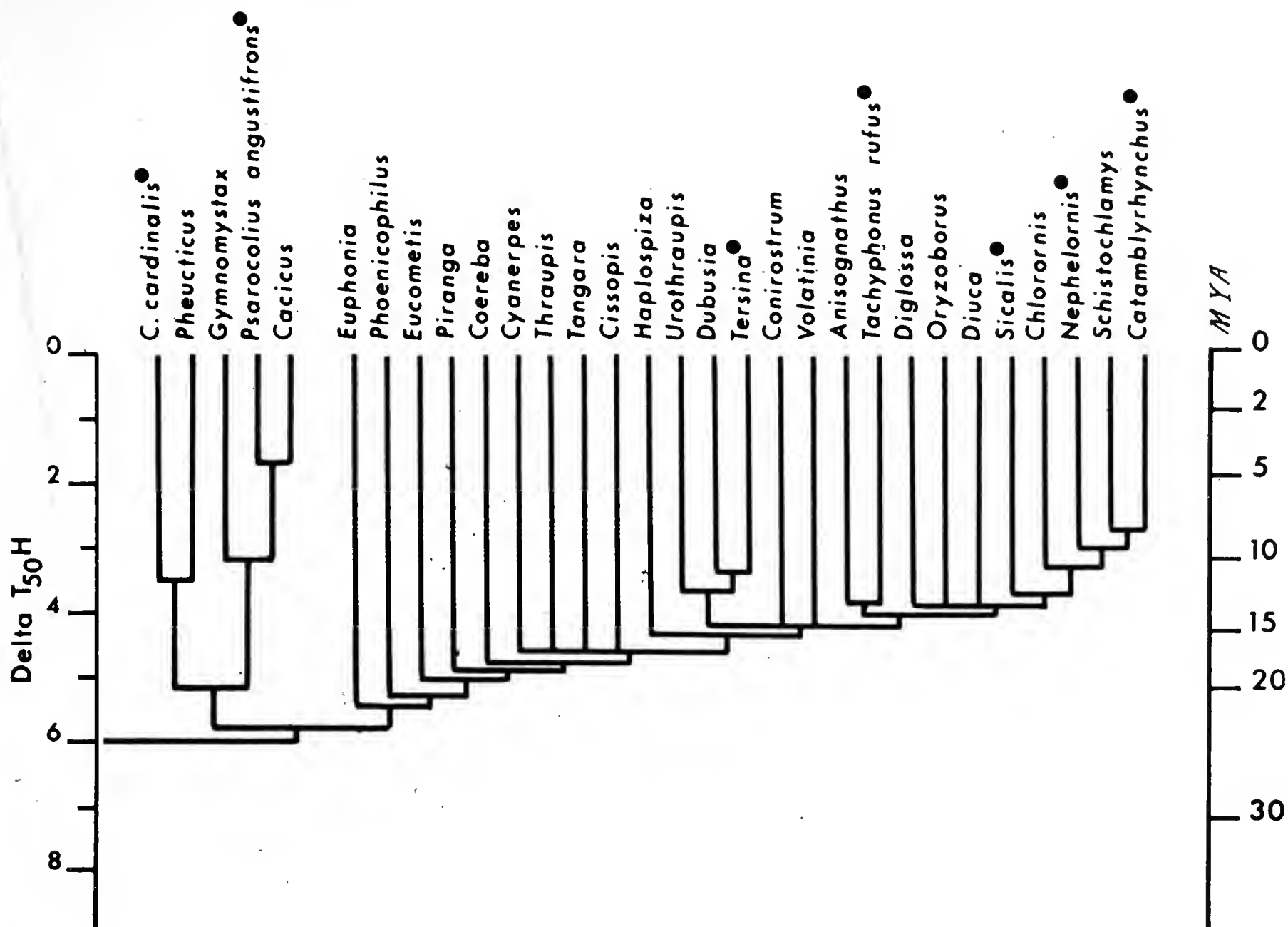


Fig. 20. Subfamily Emberizinae: Tribes Cardinalini, Icterini, and Thraupini

common ancestor of the Passerinae and the other ploceids divided into two species. The living genera of Passerinae are Passer, Petronia, and Montifringilla. We lack DNA of Montifringilla but Passer and Petronia, at $\Delta 3.3$, are closely related.

Bock and Morony (1978) found a unique skeletal structure, the preglossale, in the tongues of the three genera of passerine finches. The preglossale is associated with a tongue muscle, the M. hypoglossus anterior, in such a way that the authors concluded that the passerine finches must have evolved from a group possessing this muscle. Because the muscle is absent in "the Ploceidae, the Fringillidae and all other higher New World nine-primaried oscines" the authors concluded that none of these groups could be ancestral to the three genera of passerine finches. We agree that the three genera identified by Bock and Morony (1978) are the only living members of the Passerinae (=their Passeridae) but we suggest that their evidence does not prove that the Passerinae are not members of the ploceid cluster. Reference to our Figs. 17-19 will show that the condition of M. hypoglossus anterior in the Nectariniidae should be determined. If the muscle is present in the sunbirds the lack of it in estrildines and ploceines means that it was lost after the other ploceids branched from the Passerinae, at $\Delta 8.0$. If the muscle is absent in the nectariniids it means that the muscle was lost after they

branched from the ploceid lineage, but was present in earlier branches, although lost in the branch leading to the Fringilloidea. These questions may be answered by determining the condition in the sunbirds, the larks, and the sylvioids. In any event, the lack of the muscle, and of the preglossale, in the living species of ploceines and estrildines does not constitute proof that they are not related to the Passerinae because these structures could have been lost after the Passerinae diverged and before the other ploceids branched from one another.

It is also pertinent to note that the gene or genes coding for a complex structure may be "turned off" but not lost from the genome. Kollar and Fisher (1980) showed that the genes for tooth enamel synthesis in birds are still present and can be activated when avian embryonic tissues are grafted to the embryonic tooth-forming mesenchyme of a mammal. The loss of teeth in birds did not result from the loss of the genes coding for dental structures, but from a change in the factors required to activate them.

Sibley (1970:85-97) reviewed the complex taxonomic history of the Ploceinae and Estrildinae. Although clearly related to one another, the degree of relationship has been uncertain. The DNA data show that they are well separated ($\Delta 7.8$) and branched from a common ancestor ca. 30-35 mya.

Sibley and Ahlquist (1981c) included the family Motacillidae in the Fringilloidea, but the analysis of additional DNA hybridization measurements indicates that the wagtails and pipits cluster with the ploceids ($\Delta 7.5$) and that subfamily status as the Motacillinae in the Ploceidae is more appropriate.

Similarly (Sibley and Ahlquist, 1981b), we placed Prunella in a monotypic family but we now consider the Prunellinae to be a subfamily of the Ploceidae. Fig. 18 diagrams these relationships and the cited papers contain taxonomic reviews, data, and discussions.

The remaining ploceids are members of the Ploceinae, as shown in Fig. 18. Sibley (1970) discussed these taxa, several of which have been placed in separate families or subfamilies by various authors. It is surprising to find that Philetairus ($\Delta 4.7$), Bubalornis (4.8), Plocepasser (5.0) and Amblyospiza (6.2) are so closely related to Ploceus. Bentz (1979) concluded from a study of limb musculature that these genera are ploceids, but he placed Bubalornis in its own subfamily, Plocepasser and Philetairus in the Passerinae, Amblyospiza in the Ploceinae, and the waxbills in the Estrilididae.

The Fringillidae includes the chaffinches, bramblings, cardueline finches and Hawaiian honeycreepers (Fringillinae), and the New World nine-primaried oscines (Emberizinae). These groups began their divergences ca. 30-35 mya ($\Delta 7.4$) when the fringillines and the emberizines last shared a common ancestor (See Fig 17 and 20.).

The Fringillinae and Emberizinae apparently represent an Old World-New World dichotomy that occurred in the early Oligocene. Later, the cardueline finches spread throughout the Holarctic and into Africa and South America. The Hawaiian honeycreepers (Drepanidini) branched from the cardueline lineage ca. 15 mya in the

Miocene (Sibley and Ahlquist (1982a). (Note: the correct spelling is Drepanidini, not Drepaninini, as in the cited paper).

Sibley (1970:98-108) reviewed the taxonomic history of the New World nine-primaried oscines and proposed a classification similar to the one indicated by the DNA data, especially with reference to the categorical ranks assigned to the included taxa. The egg white protein electrophoretic patterns and the DNA hybridization measurements both reveal the extremely close relationships that exist among these groups. In Figs. 17 and 20 we have indicated dichotomies at mean delta values of 5.8, 6.0, and 6.2 between the tribes of the Emberizinae. Although these averages are based on sample sizes of from 9 to 47, and have standard errors of ± 0.2 or less, we cannot be certain that the branching sequence was exactly as depicted and, with additional data, the details may change. However, it seems probable that the emberizine subgroups branched from one another over a period of less than 5 my (ca. 23-26 mya) in the Oligocene. The divergences within the tribes continued, producing the dense pattern of dichotomies represented in Fig. 20. The delta values within the Thraupini are mostly based on single DNA comparisons and should, therefore, be viewed as having probable errors of ± 0.5 .

The DNA comparisons among the tanagers (Thraupini) revealed that they constitute a major Neotropical radiation which had not previously been recognized. An examination of Fig. 20 will show that the Plush-capped Finch (Catamblyrhynchus), the Swallow Tanager (Tersina), all of the Neotropical honeycreepers ("Coerebidae"), and several "emberizine" finches (Sicalis, Diuca, Oryzoborus, Volatinia, Haplospiza) are tanagers. These taxa are not even the most "aberrant" members of the Thraupini for they are closely related to various "typical" tanagers and the most distant members of the Thraupini are themselves "typical" tanagers.

The diagram of the Thraupini in Fig. 20 is instructive but only five taxa have been radio-labeled and the diagram is not a phylogeny of the tribe. Additional Neotropical "finches" may prove to be tanagers, and we do not know how the nectar-feeders (Diglossa, Conirostrum, Cyanerpes, Coereba) are related to one another.

It seems clear that the ancestral tanager found many empty ecological niches when, in the late Oligocene, it arrived on what was then the island continent of South America. The subsequent adaptive radiation of the tanagers has many parallels with the Galapagos finches, and with the Hawaiian honeycreepers, which also include finch-billed and nectar-feeding ecotypes.

It is gratifying to fulfill the prediction that such radiations "must exist on the continents, as they do in the Galapagos and Hawaiian archipelagos, but we should not expect to be able to delineate them by characters of the bill, the palate, the jaw muscles, the digestive tract or any other structure intimately concerned with feeding. A classification based upon such evidence cannot avoid being, in part, a classification of food niches" (Sibley, 1970:108).

The Cardinalini and the Icterini may be more closely related to one another (45.2) than are any two of the other emberizine tribes. However, this node is based upon only five comparisons and should be considered tentative.

From a study of the appendicular myology of the New World nine-primaried oscines Raikow (1978) concluded that the "affinities of the vireos are still obscure" and proposed a classification in which he recognized, as families, the Parulidae, Thraupidae, Fringillidae (with subfamilies Cardinalinae, Emberizinae, Fringillinae), Drepanididae, and Icteridae.

Historical Biogeography

The DNA-based phylogeny of the passerines, and the geological evidence of continental drift since the Cretaceous, make it possible to reconstruct a partial biogeographic history of the Passeriformes.

The passerines presumably shared a common ancestry with some non-passerine group in the Cretaceous, ca. 100 mya, but at this time we will not speculate about the possible sister group of the Passeriformes. The first dichotomy in the early passerine stem, ca. 90 mya, gave rise to the lineages leading to the Oligomyodi and the Passeres. The ancestral suboscines apparently ranged across the southern protocontinent of Gondwanaland and the divergences between the New World and Old World lineages were coincident with the breakup and drift of the southern continents. The New Zealand wrens were isolated by the opening of the Tasman Sea, ca. 80 mya, and the New World Tyrannides diverged from the Old World Eurylaimi ca. 75-80 mya, probably because the Atlantic Ocean had become too wide for interchanges between what are now Brazil and West Africa. The causes of the later dichotomies among the suboscines are more difficult to explain.

The divergence between the ancestors of the Corvi and Muscicapae occurred ca. 55-60 mya, in the Paleocene. The oldest branches within the Corvi are those that produced the living Australo-Papuan endemics: the Menuroidea, Meliphagoidea, and Corvoidea. These three groups branched from one another in the early Eocene, between ca. 48 and 53 mya. Because most of the living Corvi are confined to Australia and New Guinea it is probable that the group originated in Australia and radiated there during its long isolation in the Tertiary, as did the marsupials. As Australia drifted closer to Asia the ancestor of the Corvini (crows, jays, magpies, etc.) "escaped" to the north and radiated in Asia and Europe. Nine genera occur in North America but only two genera got to South America, and three genera occur in Africa. The living Corvus of Australia are the descendants of recent immigrants from Asia (See Fig. 11).

The Australian orioles and cuckoo-shrikes (Oriolini) are also recent immigrants whose ancestors came from Australia and radiated in Asia and Africa. The monarchs, drongos, and fantails (Monarchinae) colonized the Pacific islands, Asia, and Africa, but also radiated within Australo-Papuasias. The woodswallows and Pityriasis (Cracticini) expanded to Asia and Borneo, and the whistlers (Pachycephalini) reached some Pacific islands and southeast Asia.

Thus Australia was the nursery of the Corvi and it seems likely that their sister group, the Muscicapae, probably radiated first in Africa and spread from there to Eurasia and the Americas. The divergence between the Corvi and the Muscicapae occurred ca. 55-60 mya, when Africa and Australia were already far

apart. We can only speculate that the common ancestor of the two lineages was present on one of the two continents and was able to colonize the other in the Paleocene. The few members of the Muscicapae that occur in Australia have arrived there during the late Tertiary, after Australia had drifted close to southeast Asia.

The Muscicapae are the most abundant oscines in Africa, Eurasia, and the Americas and the Turdoidea probably originated in Africa. They branched from the sylvioid-fringilloid lineage ca. 50-55 mya and are most diverse today in Africa and Eurasia. The only suprageneric groups of turdoids endemic to the New World are the Dulini, Ptilogonatini and Mimini.

The Sylvioidea are also mainly Old World, and presumably originated there. Only the Troglodytinae and Polioptilinae are obviously of American origin. The only sylviids in the New World are Phylloscopus borealis and Chamaea fasciata.

The Old World fringilloid lineages are considerably older than those in the New World, so the group must have originated in Africa or Eurasia, ca. 45-50 mya when they diverged from the Sylvioidea. The earliest branch in the Fringilloidea occurred ca. 40-45 mya when the lark lineage diverged from the ancestor of the other three lineages in the Eocene. The Nectariniidae probably originated in Africa because the Promeropinae represent the earliest branch at 35-40 mya. However, most of the nectariniine radiation occurred in southeast Asia, producing the spider-hunters and flower-peckers, as well as various sunbirds.

The Ploceidae, which includes the sparrows (Passer), waxbills, wagtails, accentors, and weavers, are mostly African in present distribution and presumably originated there.

The Fringillidae are the descendants of a branch from the ploceid lineage, ca. 38-40 mya. The Fringillinae and the Emberizinae diverged ca. 28-30 mya and the Holarctic emberizines and Nearctic parulines radiated in North America. The Neotropical Cardinalini, Icterini, and Thraupini shared a common ancestor with the parulines ca. 20-25 mya and radiated in South America while it was an island continent during most of the Tertiary.

Discussion

We find the DNA hybridization data compelling and we believe that they provide the best available evidence for the reconstruction of the phylogeny of living birds. But traditional ideas are tenacious and changes in familiar concepts are not readily accepted. It is therefore necessary to offer empirical evidence, in addition to theoretical arguments, to support our suggestion that the measurements produced by this method are more informative as evidence of phylogenetic relationships than traditional characters.

First, the DNA-based phylogenetic trees are internally consistent and data from additional labeled taxa do not perturb previously determined nodal values. This consistency is a product of the uniform average rate of DNA evolution which also is manifested by the equal branch lengths on the two sides of any node. The

relatively small experimental error adequately explains departures from perfect reciprocity.

Second, the DNA measurements are consistently congruent with other kinds of evidence. In every case where the DNA data have departed from a traditional view of avian relationships we have found congruent morphological and/or other characters. For example, the starlings and mockingbirds share characters of the skeleton and syrinx and have similar tissue proteins (Stallcup 1961; Sibley and Ahlquist, in press a). Also, the syringeal and sternal morphologies of the New World suboscines are congruent with the DNA data for these groups (Heimerdinger and Ames, 1967; Ames et al., 1968; Ames, 1971; Sibley and Ahlquist, in press b). In addition to the DNA data, the lyrebirds and bowerbirds share an array of behavioral characters (Sibley, 1974) and the close relationships among the plumed birds-of-paradise indicated by the DNA comparisons are reflected in their ability to form natural hybrids (Sibley, 1957; Diamond, 1972).

Congruence with earth history is another source of evidence that supports the validity of the DNA hybridization measurements. The virtual restriction of the Corvi to Australia and New Guinea parallels the marsupial radiation and both radiations are clearly related to the long isolation of Australo-Papuasias from other continents during the Tertiary.

There are many other examples: the Old World broadbills and pittas are more closely related to one another than either is to the New World suboscines; the ancient divergence of Acanthisitta is congruent with the dating of the opening of the Tasman Sea; the sittellas are related to the Australo-Papuan whistlers, not to the northern nuthatches; the New World gnatwrens (Microbates, Ramphocaenus) and Verdin (Auriparus) are more closely related to other New World taxa, than to Old World groups (Fig. 16).

We hope that additional congruencies (and incongruencies) with zoogeography, morphology, and other characters will be called to our attention. We also solicit help to obtain the DNAs of taxa still missing from the comparisons.

Summary

The technique of DNA-DNA hybridization was used to compare the degrees of nucleotide sequence similarity between the genomes of ca. 800 species of passerine birds, representing all but three of the families of the Order Passeriformes. Approximately 10,000 DNA hybrids were examined and ca. 150 species were radio-labeled with Iodine-125 and used as "tracers."

A phylogeny of the Passeriformes was developed from the DNA comparisons and a classification was derived from the phylogeny. The phylogeny is presented in twenty figures and the classification in Appendix 1. Some of the results were as follows.

The Passeriformes are divided into two suborders, Oligomyodi for the suboscines and Passeres for the oscines. The Oligomyodi are subdivided into three infraorders, the Acanthisittides for the New Zealand wrens, the Eurylaimi for the Old World pittas, broadbills, and, presumably, the philepittas, and the Tyrannides for the New World suboscines. The Tyrannides are divided into three parvorders: the Tyranni includes the family Tyrannidae (Tyranninae, Tityrinae, Cotinginae, Piprinae), and the family

Mionectidae which includes a group of genera previously thought to be tyrannines, viz., Mionectes, Leptopogon, et al.

The parvorder Furnarii includes the Furnarioidea (Furnariidae), and the Formicarioidea (Formicariidae=the ground antbirds; the Rhinocryptidae; and the Conopophagidae).

The parvorder Thamnophili (Thamnophilidae) contains the typical antbirds. This group branched from a common ancestor shared with the Furnarii before the furnarioids and formicarioids branched from one another.

The suborder Passeres contains 4177 species in 823 genera. The DNA comparisons indicate that these may be divided into two parvorders, the Corvi, including the superfamilies Menuroidea, Meliphagoidea, and Corvoidea, and the Muscicapae, including the superfamilies Turdoidea, Sylvioidea, and Fringilloidea.

The Corvi are mainly restricted to Australia and New Guinea, with a few representatives in other parts of the world. The lyrebirds (Menuridae) and bowerbirds (Ptilonorhynchidae) are related to one another, but not closely related to the birds-of-paradise (Paradisaeidae). The treecreepers (Climacteridae) are descendants of an early branch in the Menuroidea.

The Australian sittellas (Daphoenositta) were shown to be related to the Australo-Papuan whistlers (Pachycephala), not to the nuthatches (Sitta), which they resemble morphologically. The paradalotes (Pardalotus) were found to be related to the Australian thornbills (Acanthiza), not to the flowerpeckers (Dicaeum) with which they have been thought to be allied. The Bornean Bristlehead (Pityriasis) is closely related to Cracticus, as also is the Papuan genus Peltops.

In the Muscicapae the chats of the Tribe Erithacini were shown to be more closely related to the Old World flycatchers (Muscicapini) than to the thrushes (Turdinae), and the starlings (Sturnidae:Sturnini) are closely related to the mockingbirds (Sturnidae:Mimini), not to the crows (Corvidae:Corvini).

The swallows (Hirundinidae), bulbuls (Pycnonotidae), and white-eyes (Zosteropidae) are members of the Sylvioidea and the sylviine warblers (Sylviini) and babblers (Timaliini) are so closely related that they can be placed in the same subfamily.

The Superfamily Fringilloidea includes the larks (Alaudidae), sunbirds (Nectariniidae), weaverbirds and their allies (Ploceidae), and the finches, buntings, troupials and tanagers (Fringillidae). The wagtails and pipits (Motacillinae) and the accentors (Prunellinae) are members of the Ploceidae.

The Neotropical tanagers (Thraupini) are a major adaptive radiation that includes the typical tanagers (e.g., Piranga, Tachyphonus, etc.) and also the Swallow-Tanager (Tersina), the Plush-capped Finch (Catamblyrhynchus) the Neotropical honeycreepers ("Coerebidae"), and several finch-billed genera (Sicalis, Volatinia, Oryzoborus, Diuca, Haplospiza) which have been thought to be emberizine finches.

The DNA data are congruent with morphological characters and with earth history in many ways, thus increasing the probability that they are providing a true picture of the phylogeny of the passerine birds.

ACKNOWLEDGMENTS

We have had the help of many persons during this study, in the laboratory and in the field. Some have been acknowledged in the papers based on DNA hybridization which are cited below. For the sake of brevity their names will not be repeated here, but we do repeat our thanks to them. We are also grateful to the following persons who have contributed to the present study: A.Archer, R.P.Balda, B.Beehler, B. and H.Bomford, J.I.Borrero, J.I.Borrero, Jr., R.Bruggers, J.R.Contreras, R.L.Crawford, A.Dod, K.Feltcher, D.Forsell, J.Forsyth, S.Furniss, P.Gertler, G.Graves, J.Haffer, L.Hammonds, J.Hechtel, R.Hutchings, B.Kaghan, C.Koford, E.Koford, S.Koster, W.Lanyon, H.Laycock, T.Lemke, G.Lester, S.Levy, G.Maclean, E.Mayr, G.Medway, W.Meise, G.Meyer, M.Morrison, J.Nadal, S.Olson, S.Parker, T.Parker, K.C.Parkes, R.B.Payne, R.Raikow, A.Ruschi, W.C.Russell, R.Schodde, D.Schroeder, T.Schulenberg, R.Siegfried, G.Smith, T.B.Smith, B.Stonehouse, G.Storr, D.Tallman, C.Vernon, L.Wallace, K.Westerskov, J.Williams, K.Wohl, H.Wolters, and R.Zink.

The laboratory work was supported by Yale University and the U.S. National Science Foundation (DEB-77-02594; 79-26746). Some material was obtained during the 1969 Alpha Helix Expedition to New Guinea, supported by the U.S. National Science Foundation via grants (GB-8400; 8158) to the Scripps Institution of Oceanography of the University of California, San Diego.

APPENDIX

CLASSIFICATION OF THE AVIAN ORDER PASSERIFORMES

Order Passeriformes

Suborder Oligomyodi

Infraorder Acanthisittides

Family Acanthisittidae, New Zealand Wrens

Infraorder Eurylaimi

Superfamily Pittoidea

Family Pittidae, Pittas

Family Eurylaimidae, Broadbills

(Family inc. sedis Philepittidae, Asities)

Infraorder Tyrannides

Parvorder Tyranni

Superfamily Tyrannoidea

Family Tyrannidae

Subfamily Tyranninae, Tyrant Flycatchers .

Subfamily Tityrinae

Tribe Schiffornini, Schiffornis

Tribe Tityrini, Tityras, Becards

Subfamily Cotinginae, Cotingas, Plantcutters, Sharpbills

Subfamily Piprinae, Manakins

Family Mionectidae, Mionectid Flycatchers

Parvorder Furnarii

Superfamily Furnarioidea

Family Furnariidae

Subfamily Furnariinae, Ovenbirds

Subfamily Dendrocolaptinae, Woodcreepers

Superfamily Formicarioidea

Family Formicariidae, Ground Antbirds

Family Rhinocryptidae, Tapaculos

Family Conopophagidae, Gnateaters

Parvorder Thamnophili

Family Thamnophilidae, Typical Antbirds

Suborder Passeres

Parvorder Corvi

Superfamily Menuroidea

Family Climacteridae, Treecreepers

Family Menuridae

Subfamily Menurinae, Lyrebirds

Subfamily Atrichornithinae, Scrub-birds

Family Ptilonorhynchidae, Bowerbirds

Superfamily Meliphagoidea

Family Maluridae

Subfamily Malurinae

Tribe Malurini, Fairy-wrens

Tribe Stipiturini, Emu-wrens

Subfamily Amytornithinae, Grass-wrens

Family Meliphagidae, Honeyeaters, incl. Ephthianura

Family Acanthizidae

Subfamily Pardalotinae, Pardalotes

Subfamily Dasyornithinae, Bristlebirds

Subfamily Acanthizinae

Tribe Sericornithini, Scrub-wrens

Tribe Acanthizini, Thornbills, Whitefaces, etc.

Superfamily Corvoidea

Family Eopsaltriidae, Australo-Papuan robins, incl. Drymodes

Family Orthonychidae, Log-runners or Chowchillas

Family Pomatostomatidae, Australo-Papuan Pseudo-babblers

Family Corvidae

Subfamily Cinclosomatinae, Quail-thrushes, Whipbirds, etc.

Subfamily Corcoracinae, Australian Chough, Apostlebird

Subfamily Pachycephalinae

Tribe Neosittini, Sittellas

Tribe Falcunculini, Shrike-tits

Tribe Oreoicini, Crested Bellbird

Tribe Pachycephalini, Whistlers, Shrike-thrushes, etc.

Subfamily Monarchinae

Tribe Rhipidurini, Fantails

Tribe Dicrurini, Drongos

Tribe Monarchini, Monarchs, Magpie-larks

Subfamily Corvinae

Tribe Corvini, Crows, Magpies, Jays, Nutcrackers, etc.

Tribe Paradisaeini, Birds of Paradise

Tribe Cracticini, Currawongs, Woodswallows, Pityriasis

Tribe Oriolini, Orioles, Cuckoo-shrikes

(Corvoidea incertae sedis)

(?Subfamily Laniinae, Shrikes)

(?Subfamily Vireoninae, Vireos, Pepper-shrikes)

(?Category Irena, Aegithina, Chloropsis, Melanocharis)

Parvorder Muscicapae

Superfamily Turdoidea

Family Bombycillidae

Tribe Dulini, Palm Chat

Tribe Ptilogonatini, Silky Flycatchers

Tribe Bombycillini, Waxwings

Family Cinclidae, Dippers

Family Turdidae

Subfamily Turdinae, Typical thrushes, incl. Chlamydochaera

Subfamily Muscicapinae

Tribe Muscicapini, Old World Flycatchers

Tribe Erithacini, Chats

Family Sturnidae

Tribe Sturnini, Starlings

Tribe Mimini, Mockingbirds, Thrashers, Catbirds

Superfamily Sylvioidea

Family Sittidae

Subfamily Sittinae, Nuthatches

Subfamily Tichodrominae, Wallcreepers

Family Troglodytidae

Subfamily Certhiinae, Northern Creepers

Subfamily Troglodytinae, Wrens

Subfamily Polioptilinae, Verdin, Gnatwrens, Gnatcatchers

Family Paridae

Subfamily Remizinae, Penduline Tits

Subfamily Parinae, Titmice, Chickadees

Family Aegithalidae, Long-tailed Tits, Bushtits

Family Hirundinidae, Swallows

Family Regulidae, Kinglets

Family Pycnonotidae, Bulbuls

Family Cisticolidae, African Warblers

Family Zosteropidae, White-eyes

Family Sylviidae

Subfamily Phylloscopinae, Leaf Warblers

Subfamily Megalurinae, Grass Warblers

Subfamily Sylviinae

Tribe Sylviini, Old World Warblers

Tribe Timaliini, Babblers and Wrentits

Superfamily Fringilloidea

Family Alaudidae, Larks

Family Nectariniidae

Subfamily Promeropinae, Sugarbirds

Subfamily Nectariniinae

Tribe Dicaeini, Flowerpeckers

Tribe Nectariniini, Sunbirds, Spider-hunters

Family Ploceidae

Subfamily Passerinae, Sparrows, Rock Sparrows, etc.

Subfamily Estrildinae, Waxbills

Subfamily Motacillinae, Wagtails and Pipits

Subfamily Prunellinae, Accentors

Subfamily Ploceinae, Weaverbirds

Family Fringillidae

Subfamily Fringillinae

Tribe Fringillini, Chaffinches, Bramblings

Tribe Carduelini, Goldfinches, Crossbills, etc.

Tribe Drepanidini, Hawaiian Honeycreepers

Subfamily Emberizinae

Tribe Emberizini, Buntings, Longspurs, etc.

Tribe Parulini, Wood Warblers, incl. Zeledonia

Tribe Cardinalini, Cardinals

Tribe Icterini, Troupials, Meadowlarks, Oropendolas, etc.

Tribe Thraupini, Tanagers, Neotropical honeycreepers,
Swallow-Tanager, Plush-capped Finch,
Tanager-finches.

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GEOGRAPHICAL AND ECOLOGICAL ASPECTS OF BIRD MIGRATION AS A METHODOLOGICAL PROBLEM

Przemysław Busse

Bird Migration Research Station of Gdansk University
Przebendowo, Poland

The bird migration is a very complicated phenomenon of many aspects. So, in the bird migration studies one can find a number of research streams, which belong to different zoological disciplines. Very often, however, they are closely connected with each other and then it is rather difficult to discuss separate aspects.

As it is fit and proper to define what we will write about, I shall try to show what part of bird migration studies will be taken into consideration (Fig. 1). The bird migration phenomenon can be studied in different aspects, symbolised by small circles situated at the great circle. These aspects are grouped because of their connections with other disciplines. In the central part of the figure there are shown the main connections between the aspects listed. In the lecture there is discussed a number of these aspects marked by a black colour in the drawing. The selected aspects do not cover the whole area of interest of ornithogeography and ecology at the field of bird migration; they were chosen because of a number of common methodical problems. The ornithogeographical and ecological aspects which were excluded from the discussion have some connections with the left ones, but the time limits make it impossible to expand the topic.

The methodical problems of the studied aspects of bird migration are to be found at all the three levels of scientific work: (1) collecting of raw data, (2) storage, exchange and technical manipulation of the material, and (3) the analysis level. The problems are of two kinds - substantial and practical, caused by the technique and/or organization of work. The substantial ones can appear at every level, the second group at the two first levels mainly, but both kinds condition each other quite a lot.

COLLECTING OF THE RAW DATA

The group of aspects selected for the lecture is studied in the field by methods of observational character. There do not exist established laboratory experiments, nor the field ones. The most popular methods are listed in the Figure 2, which is cited after the lecture presented several years ago at the Second Baltic Conference in Sopot, Poland. There was analysed contents of nearly 400 papers on bird migration published in northern Europe and America in the period 1967-1976. Not all these methods are equally often used. Especially papers from the journals of some countries show a preference for particular methods. The blocks at the right show these special preferences.

What are the methodical problems at the level of raw data collecting?

The most popular method - the ringing seems to be nonproblematic at first sight: the bird must be ringed with a proper ring. But there arises a serious problem of substantially-practical nature: what birds should be ringed? Different ringing centres face a lot of trouble with money and/or with the technical possibilities of recovery elaboration. This imposes a number of limi-

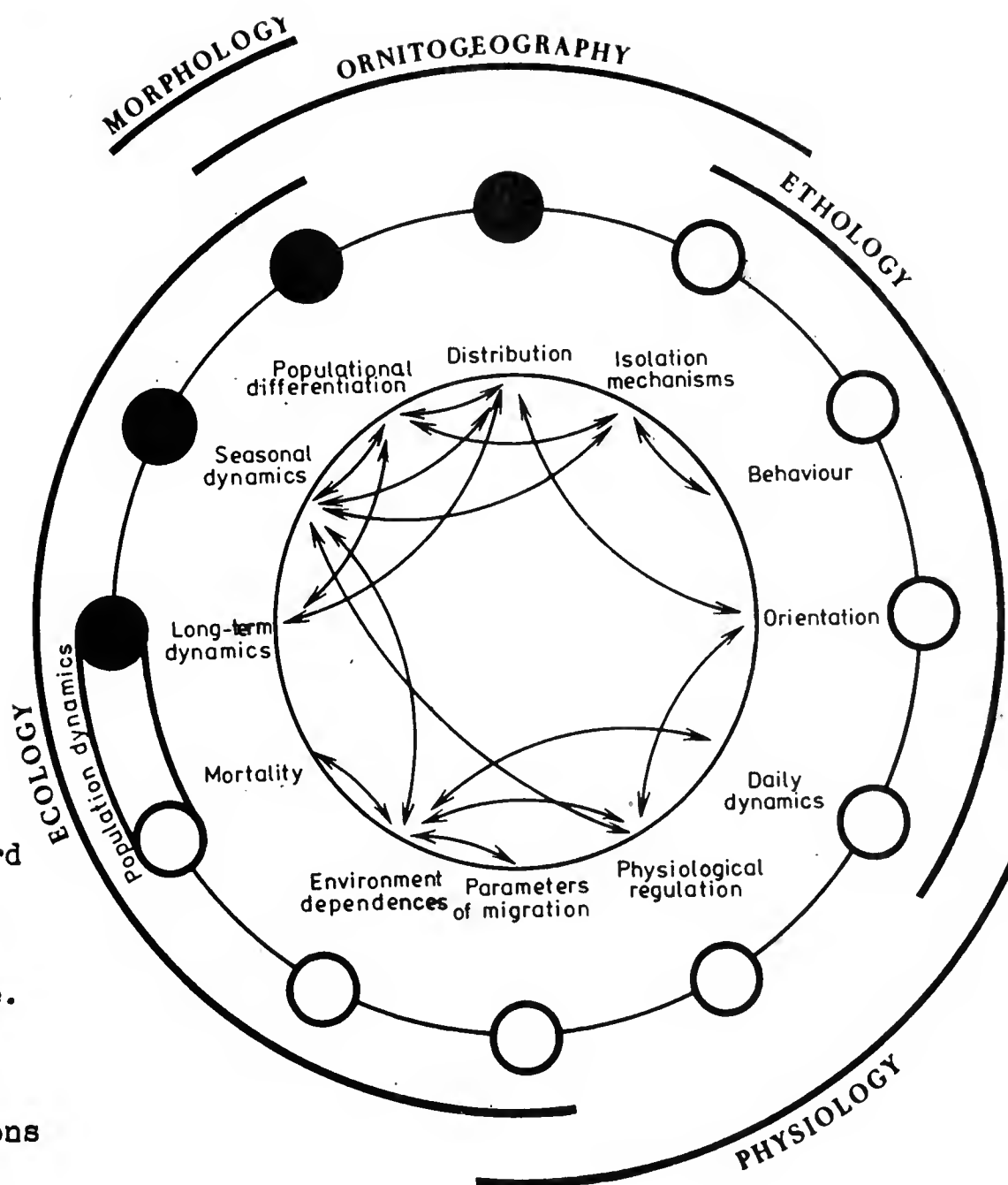


Fig. 1.
Different aspects of bird migration studies.
Black colour - aspects discussed in the lecture.
In the central part of the figure there are shown the main connections between the aspects

tations on ringers' activity. The most common solution of the problem is to suspend ringing of more numerous species, which have given "enough" recoveries. I have written the word "enough" in the quotation marks, because I cannot agree with the opinion that any species from any territory in the world, has really yielded a sufficient number of recoveries. This word could be used in this context in its relative meaning only: the number of recoveries of this species is sufficient to describe the average distribution only, or the average course of migration or the average survival rate. When we limit our interest to such classical and primitive questions, we are right. But the essence of science is putting forward and newer questions. So, the mentioned self-limitations mean the end of the scientific work. Consequent adhering to this policy for years may lead us to the moment when we shall say: our knowledge about all the species is roughly similar, but in absolute dimensions it is next to nothing. It will be the moment when ringing as a method will lag far behind the other streams of migration research. The problems solvable with really rich data, collected year by year will be impossible to study. Who will be able to answer such questions as:

What is the extent of yearly changes in winter-quarters and the mortality rate?

Is the detectable evolution of winter-quarters and routes of migration caused by changes of the environment provoked by man?

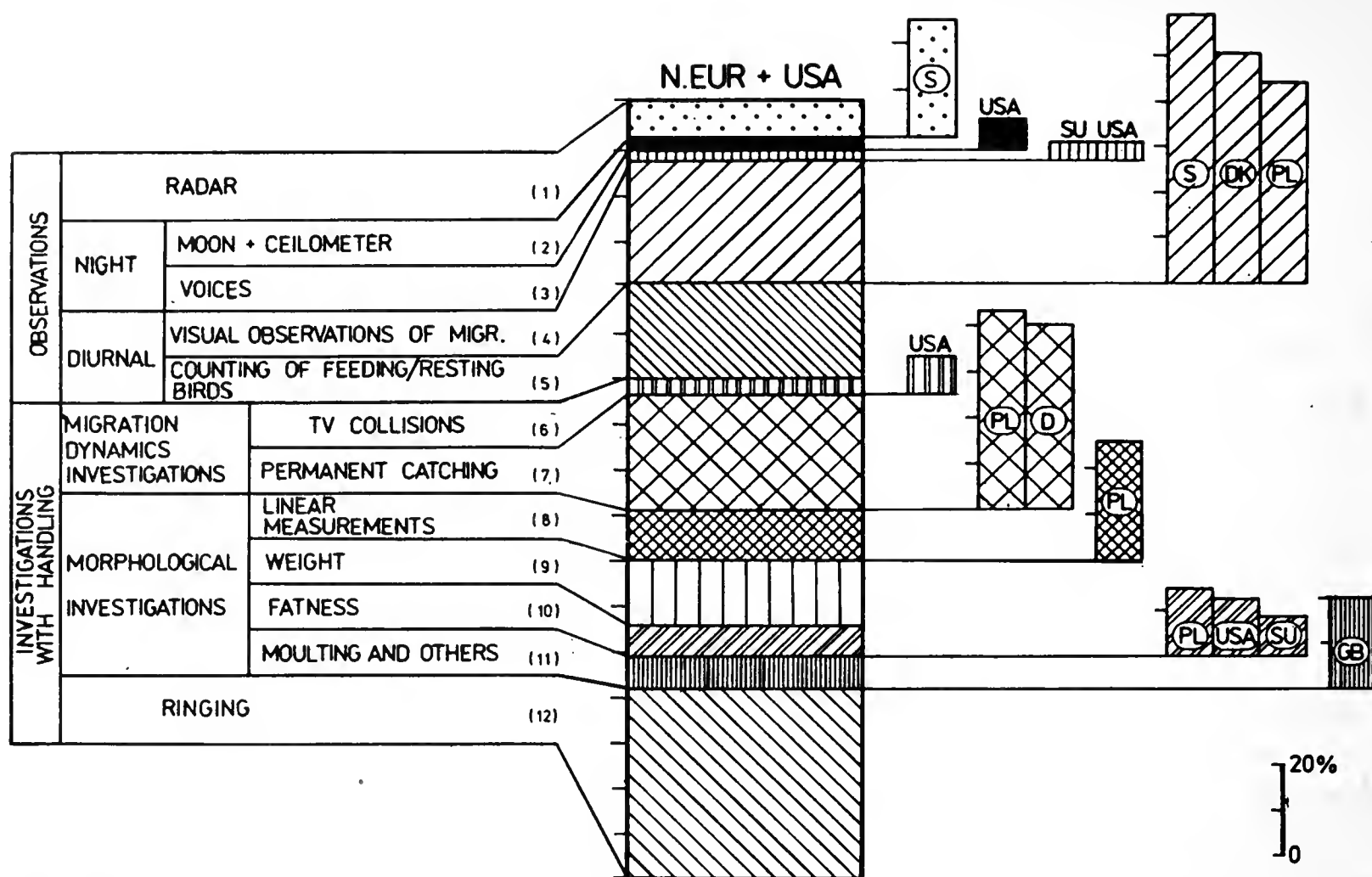


Fig. 2. The classification of the field methods and frequency of their usage in studies published in the papers surveyed. N.EUR - Northern Europe, S - Sweden, SU - Soviet Union, DK - Denmark, PL - Poland, D - Federal Republic of Germany, GB - Great Britain (after Busse, Kania, 1980)

What are the mechanisms of partial migration and irruptions? and so on, so on ...

Let us try to check, from the point of view of analyst, which groups of ringed individuals give the most valuable recoveries. I have no doubt that they are: native birds (pulli and breeding adults) and wintering birds. The first group contains about 30-35% of birds ringed in most of the European countries, the second one - I guess - about 5%, so both together 40% at most. It means that 60% of the rings is used during the unstable period of wandering and migration. The most of them - by weekend ringers and by those ringing stations which do not follow any defined program of migration studies. This last one is the group of wasted rings. The information obtained by such accidental ringing is incommensurate to the effort of the ringing centre.

The conclusion could be only one: to stop the accidental ringing of all species, but to continue the useful ringing of all birds. This result in a more scientific and less sportish work of bird stations.

In visual observations of the passage there are no important problems. The method is simple, although the observers must be highly qualified. Accidental observations are not accepted as the data for bird migration analyses. The only problems are connected with organization of work of the stations. In this connection the observations may be continuous with in the period of some hours or organized as sample observations throughout the day. Both variants are highly correlated and they are comparable.

The results of a continuous, or in other words , quantitative catching are used as source data in the description of dynamics of the passage or for long-term dynamics studies. The first application is simpler from the organizing point of view - the number and quality of catching instruments (nets, traps etc.) must be stable during the season and they must work permanently. The long-term studies are more requisite as the effectiveness of the set of catching instruments must be comparable throughout the subsequent years which is difficult to attain. One possibility is to strictly stabilize the environment by cutting the bushes or trees in the catching area, as eg. it is done at Mettnau station. This method is very laborious and effective in some habitats only. The additional trouble lies in the fact that the habitats surrounding the stations are observed in succession, which affects the results too. The second method - active compensation of changes of effectiveness by dislocation of nets or traps according to the changes of habitat, as it is done at the Polish Operation Baltic stations, is less precise, but the errors seem to be much lower than the observed long-term changes in the number of migrants.

Counting of feeding or resting birds as a basis for the study of migration dynamics is closely related to visual observations, but somewhat more labile. Local topography, habitats or ecological group of birds under observation decide about the variant of the method. In this method stability of the area or transection and the time parameters of the control are as important as the permanency of work. Accidental observations or controls at some day intervals are of no use, exactly as in visual observations or quantitative catching.

The problems with the use of biometrical methods in the field are relatively few. The technique of measurements is rather simple and there is a hope for high degree of standardization in the near future. The set of measurements which are done at the station is, however, very variable. In the most cases there are collected wing-length and weight data. They are collected, but rarely used for more advanced studies. The reasons of this phenomenon will be discussed later.

Most of the data for migrational studies are collected at permanent or temporary ringing stations, which have various conditions, histories, organization and scope of work. There are comfortable stations and well equipped laboratories with a relatively narrow scope of used field methods. There are medium standard living conditions and rather ineffective work-methods of the "walking laboratory", and there are primitive camp conditions and relatively or even highly comprehensive program of work in the nearly open air laboratory. As an example, the work-schedule of an Operation Baltic station can be mentioned. There are carried out sample visual observations (15 minutes per hour, all day), quantitative catching (about 50 nets, with up to 3 thousand of caught birds per day), ringing and some biometrical measurements (wing-length, tail-length, quantitative wing-formula, fatness discrimination and weighting) of all caught birds.

So, I would like to formulate the conclusion, that the scope of station work depends more on scientific conceptions and organization of work than on the financial, technical and living conditions. As you can easily guess, I am a devotee of as complex studies of bird migration as possible. Moreover, this

complexity should be equally wide both in the field and at the level of analysis. At this moment I would like to propose, as the first key-world of bird migration studies, the term: "Complexity".

STORAGE, EXCHANGE AND TECHNICAL ELABORATION OF DATA

Collecting of data for simple, one method - one problem analysis could be done by means of primitive recording tools - a pensil and a blank sheet of paper. More complex data must be effectively recorded in special notebooks or on cards adapted to direct punching or taping for computer elaboration. This requires construction of such coding systems which would be clear and easy to use in the field. And that is the weak point of many research programmes.

Moreover, the recorded data must be exchangeable - it is a necessity arising from the trend visible in bird migration papers published recently - there are more and more analyses based on the data obtained from a great number of various stations.

Here we encountered the greatest problem at this level of work, which has to be solved if we want to have a more pronounced progress in the bird migration research. In the way to exchangeability of the data, there stand some serious obstacles. They are as follows:

1. Different histories, different concepts and circumstances of work at the stations and isolation of teams. The concepts of work at the stations are strictly adapted to local conditions and local habits of ringers and bird-watchers.

2. No logical analysis of problems studied. The methods and forms used are usually the result of evolution of the work at the station. It is surprising that the routine work of so many stations contains elements which are completely unpractical and illogical.

3. Localisms and psychological barriers. This kind of obstacles is the hardest problem of co-operation on a national and international scale. Combined with the two preceding phenomena, localisms force the creation of quite unusable systems, incomparable with anything existing.

The general direction of organizational activity in the field of bird migration research should go towards the elimination of substantial methodical differences between stations. The wide circulation of information at the national and international level, more intensive personal contacts and propaganda work eliminating the localisms would be the main tools. Carefully prepared standards, based on great experience and logical analysis of the work structure, are usually much more effective and they really save time and manpower. The essential problem lies in the comparability of the data, which does not automatically mean identity of data format and data set.

The real progress in this direction has been made by the New-EURING Code for ringing and recovery data. It could be an excellent starting point for the construction of practical coding systems, which will allow of easy and direct coding of data in the field.

THE ANALYSIS

At the outset of this discussion, let us check to what an extent the aspects of bird migration, which are of interest here, are popular in the published studies. The data cited are taken from the previously mentioned analytical lecture at Sopot Conference. The seasonal dynamics was presented in 48% of the papers and distribution in 46%. Two other aspects discussed here are surprisingly rarely studied - long-term dynamics in 13% of papers and populational differentiation in 8%. After this finding the basic question arises: is this picture the reflection of scientific importance of the aspects? My answer is simply: no.

It is very characteristic that the most popular aspects are presented in publications mostly as a description of facts and not as deeper analyses leading to any synthesis. This is the simplest mode of paper writing. The equally characteristic sign is that the most complicated, as to methodical requirements, aspect - the populational differentiation analysis - is equally rare as presentation of the new methods. It is the sign of a dangerous inertia in bird migration studies. This statement is confirmed by the fact that as many as 7% of the papers present raw material, without any conclusion.

The other sign of the alarming conceptional stability is the mode of presentation of ringing results, which has remained the same since 1931 Schüz and Weigold atlas (Schüz, Weigold, 1931). Apart from some similarities in the illustration technique, in most cases there are shown maps of monthly distribution of ringed birds' recoveries and formally delimited geographical territories. This very classical, but not biological, treatment is surprisingly stable, even in the synthetic maps, as eg. in a most voluminous ringing analysis - the paper on Lapwing migrations in Europe. The syntheses of bird migration studies presented as the maps of population distribution are published sporadically (Fig. 3).

What is the reason of this situation? The reason is, in my opinion, the lack of clear conception of what we want to know, from the ornithogeographical and ecological points of view, about migrant species.

Here I would like to propose the choice of second key-word for the discussed aspects - the words "populations' differentiation".

At the beginning of any further discussion we must delimit the meaning of this term so widely used. The word "population" alone does not define what we happen to be thinking of a given moment about, but it denotes a set number of meanings, all of them basing on a silent assumption that there is a kind of intraspecific differentiation.

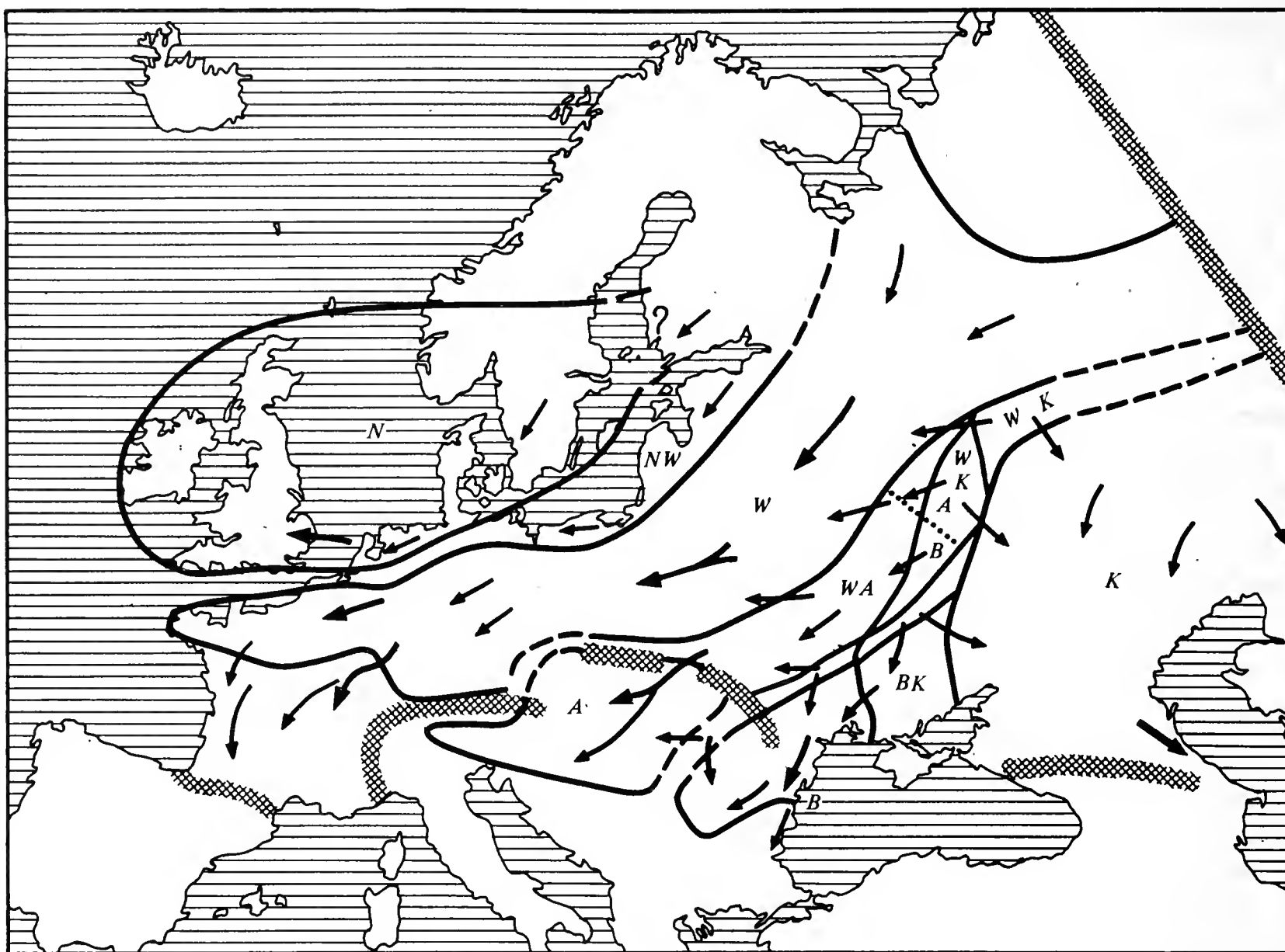
From the ornithogeographical point of view one can speak about:

- phylogenetical populations - the groups of birds, which are of common origin, if in the phylogeny of the species there were periods of genetical isolation;

- migrational populations - the groups of birds, which can be characterized by common migrational habits, usually different winter-quarters or a different migrational route.

The morphological point of view suggests a distinction of

- morphological populations - the groups of birds, which are differentiated by morphological, usually biometrical parameters. This is used when diffe-



F i g. 3. Populational differences of European Rooks. Heavy line and one-letter signs - areas occupied by pure populations; thin line and multi-letter signs - mixed zones between populations; broken line - estimated interpopulational boundaries; dotted line - subpopulational boundaries; arrows - directions of migration; crossed line - main mountain ridges (after Busse, 1969)

rences observed are smaller than accepted for a subspecies level of differentiation. It is a meaning very close to the phylogenetical one, yet we must remember that is is not the same.

From the ecological point of view we can distinguish demographical, or breeding populations, characterized by common population dynamics.

The relations between these divisions are not clear yet, but all these structures are important enough to remember them, both from the theoretical and practical point of view.

If we agree with the theory that migration habits are the reflection of the history of the populations' invasion into the present breeding territories, we must treat most of the migrational populations as the phylogenetical ones. Some of the migrational differences can, however, be of a more recent, ecological origin.

More complicated relations can be assumed between phylogenetical and morphological populations. It is easy to imagine that groups of birds of different origin and, at the same time, differentiated genetically, are differen-

tiated morphologically too, but it is possible that actual selection pressure has changed original morphological characteristics of groups and smoothed away differences into clinal ones.

Probably the most independent classifications are the phylogenetical and ecological ones. The latter are most obviously dependent on actual habitats - their geography, climate and other ecological relationships. However, the genetical background of population vigor cannot be neglected.

Between different populations there can occur complicated interactions - they can be isolated from each other more or less clearly in breeding or winter areas and/or in the route, but they can appear jointly at least at some areas or during migration period. The example of the first possibility was presented in the Figure 3. The more complicated picture was found in unpublished yet study on migrational differentiation of the north European Song Thrushes. Four migrational populations are mixed there to a great extent at the breeding grounds and their migrational routes coincide partly or cross each other. Moreover, the biometrical structure of this species is independent of the migrational one. These phenomena complicate migrational studies very much, but make one aware of the risk of generalizations made of the basis of a single study: there are too many possibilities. I am sure, that some heated discussions between representatives of different research schools could be much simpler if the multifarious character of populational structures were clearly understood.

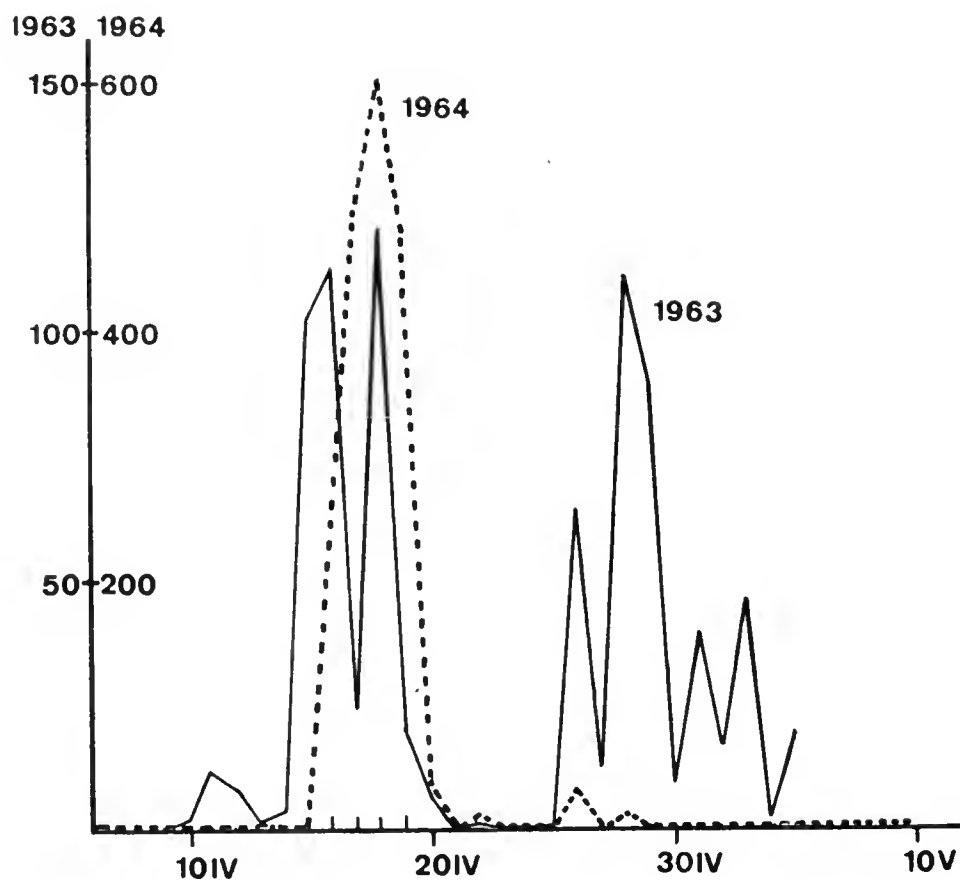
What are the methodical consequences of present situation?

I think that it is a fundamental rule, that populational differentiation must be taken into consideration in practically every migrational analysis. In many studies this line of approach clears the results, in other ones it saves the authors from the sheer nonsense, such as eg. calculating mean geographical position of recoveries, when two or more populations are involved. For this reason all the possible methods of population identification should be used whenever possible. Unfortunately, most of the existing methods do not solve the problem when they are used individually. Many of them must be cross checked by combining with the other ones.

At this moment it should be stressed that most of the papers published recently present the results obtained by the use of one method only. This is about 65% of papers on the average (Busse, Kania, 1980). The highest complexity of papers was found in Great Britain (1.65 field method per paper) and Scandinavia (1.56), the lowest in FRG (1-27) and Danemark (1.13). Generally the complexity of studies is much too low.

Now, I would like to review some examples of the new analytical methods by different aspects studied.

The most popular aspect - the seasonal dynamics is presented usually in the very passive manner. Mostly, there is a description of the course of migration and nothing more. Although the graphs or histograms presented are always very irregular, the analysis of the causes of this phenomenon is the rare case. Usually these irregularities are generally explained by meteorological dependences of migration and sometimes only by physiological or populational causes. This last interpretation is rare because usually it is impossible to prove a hypothesis using one method only. The analysis of seasonal dynamics



F i g. 4. Spring migration of Coal Tit at Hel (Poland) in the years 1963 and 1964 - daily dynamics of passage (results of catching), after Busse (1978)

data, collected by quantitative observations or quantitative catching methods can be, however, the starting point for further work based on other methods. Such methods as recovery or biometrical studies, could usually verify the hypotheses formulated on the basis of "waveness analysis".

What is meant by "waveness analysis"? If one has the graph illustrating seasonal migration dynamics by days, and only by days, one can try to divide it into blocks of days with intensive passage, separated from each other by low migration days. In such clear cases as on the Figure 4 it is rather easy work, especially if it was known that the decrease of migration was not caused by the weather. The same figure illustrates the possibility of verification of the wave discrimination by repeating this procedure in the other year (or at another station situated not far away). If the distinguished waves represent groups of birds characterized by relatively stable season of migration (which commonly is the case) the homologization of waves through the subsequent years can be possible. This operation opens the chance to verify the hypothesis of populational character of the waves by means of biometrical and ringing methods. The Figure 5 shows an example of many year wave homologization. The picture presents border days of waves formed by Song Thrushes migrating through the Polish Baltic coast. The raw material for this analysis were the results of quantitative catching by mist nets. This wave division was checked by means of visual observations data and by analysis of retraps, which prefer to leave the station area before the next wave arrival. The differences between these three methods of waveness analysis can be neglected (see Fig.5).

The analysis of recoveries based on waveness of migration previously mentioned gives an irreplaceable possibility of quantitative treatment of ringing data. The method of quantitative estimation of ringed birds distribution on the basis of recovery dispersal was published not long ago (Busse, Kania, 1977). The general problem of this method is as follows: if the group of ringed birds is dispersed to different winter areas, the number of recoveries

Fig. 5. Homologization of migrational waves of Song Thrush at Polish Baltic coast. Border days between the waves are shown: ● border days fixed by use of three methods; ○ - border days suggested by analysis of catching results only. P - number of pentade (after Maksalon)

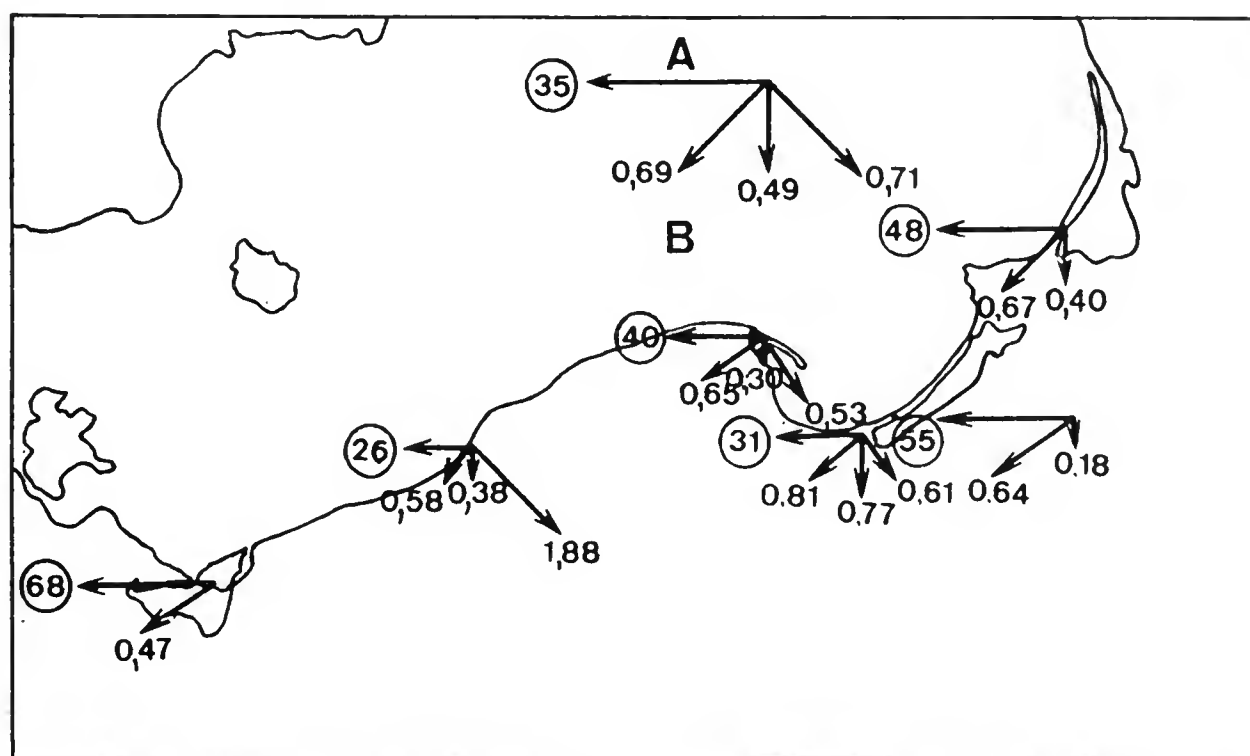
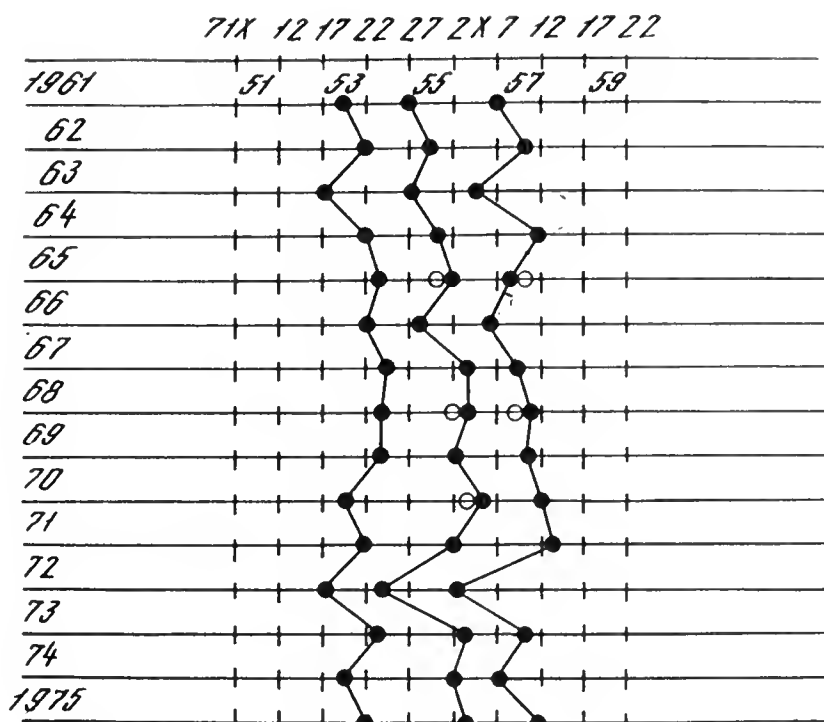
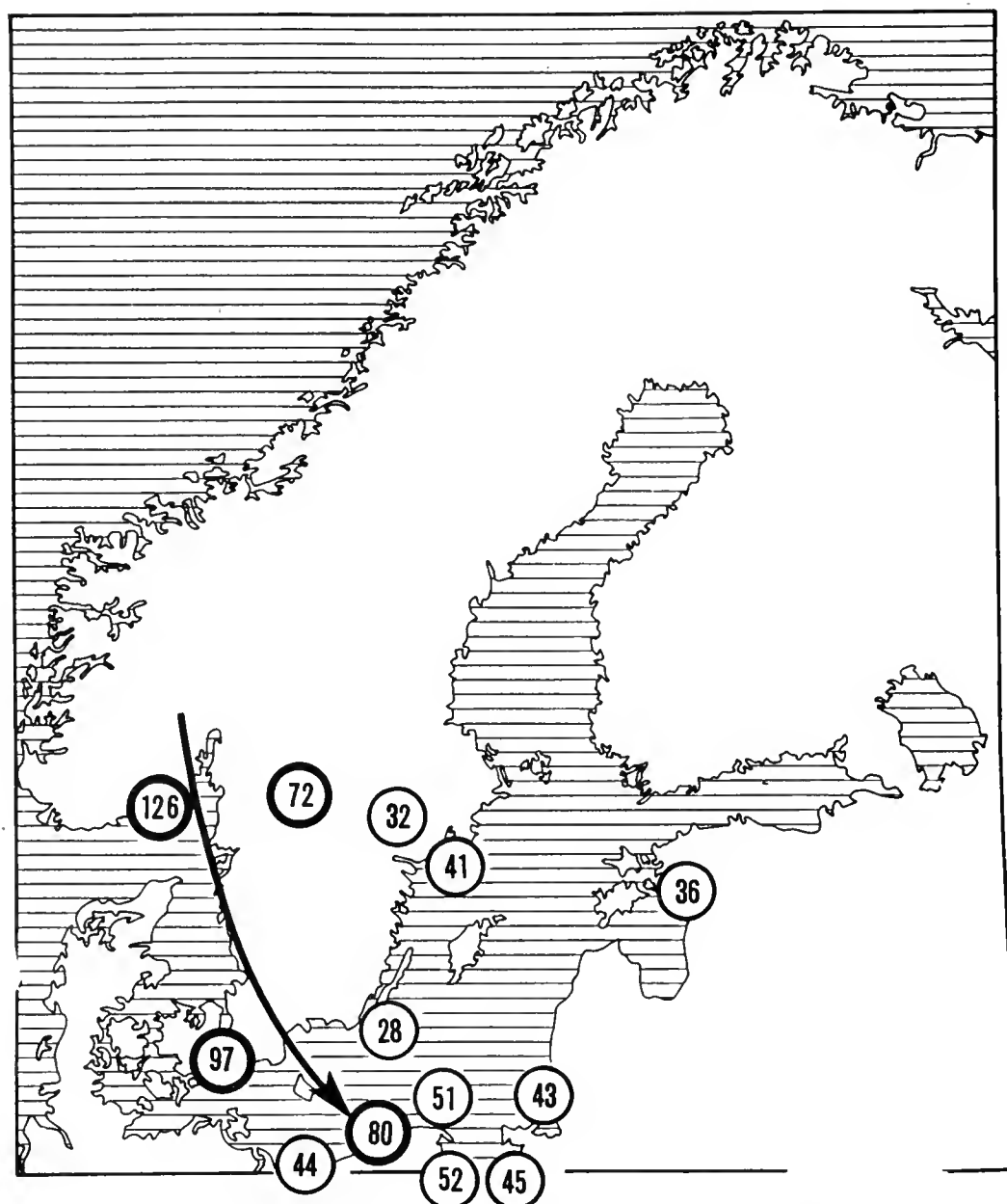


Fig. 6. Frequency of Song Thrushes directing to four winter-quarters (called W, M, E and EE). A - grand total for all the Polish stations together; B - distribution at the stations. In the circles - per cent of birds heading to W territory, other arrows described by numbers being the relation of number of birds heading to M, E and EE territories to number of birds heading to W territory. After Busse, Maksalon (1978)

from these usually does not reflect the real proportions, in to which the birds are divided. It is because of different chances of recovery from these areas, caused by many factors, biological and human ones. The only way to obtain the real picture of distribution of birds is to analyse the recoveries from individuals ringed at some stations or in subsequent waves of migrants, if they are distributed in the studied areas in different proportions and if the number of ringed specimens is known. It is too short time for a more detailed presentation of this method and only one example can be shown. The Figure 6 illustrates the proportions of Song Thrushes migrating to different winter-quarters through different south Baltic bird stations.

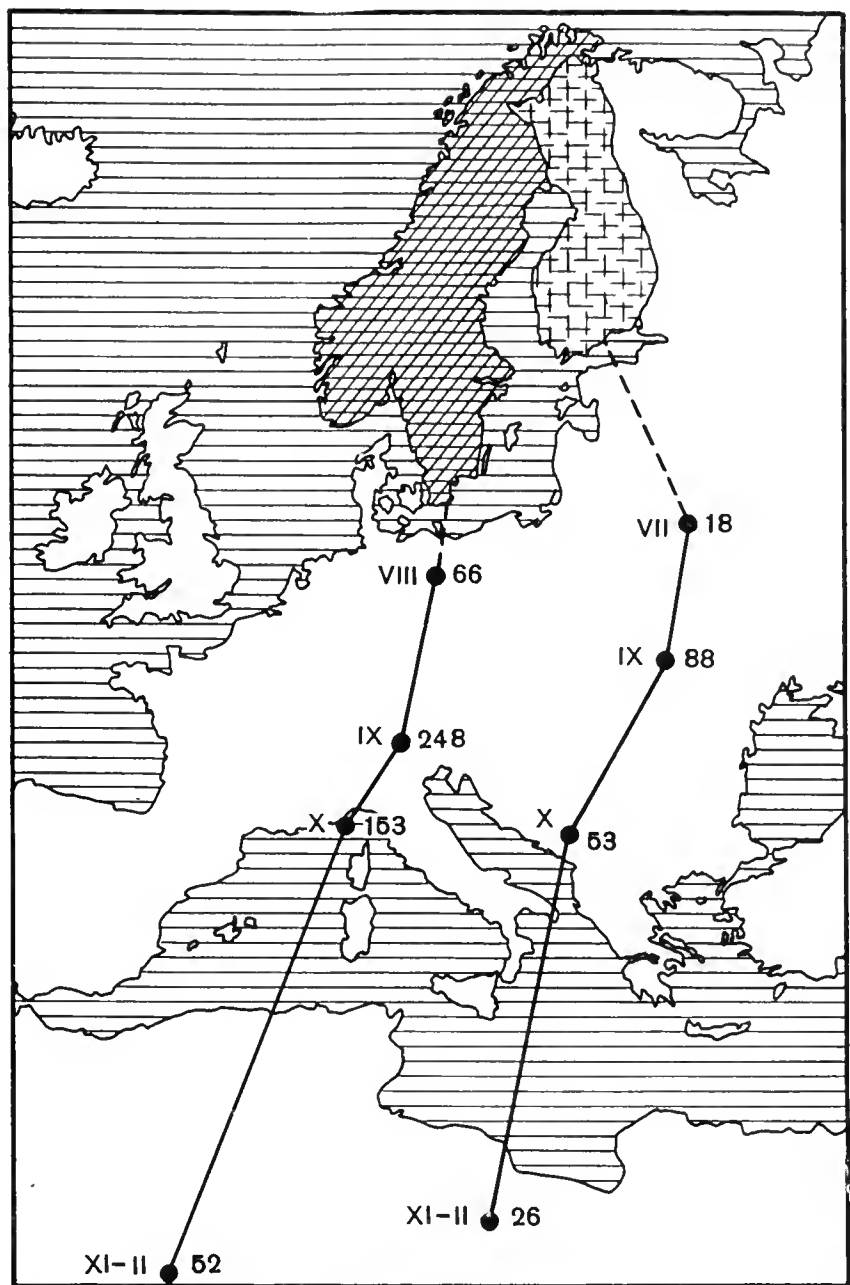


F i g. 7. Suggested direction of migration of Song Thrush population directing to Balkan Peninsula, where the detectability of ringed birds is very low (high number of birds must be ringed per one recovery). In the circles - number of ringed Thrushes per one recovery at different bird stations. The thick circles are used for the stations of much higher values of this index

The other method of quantitative treatment of ringing data was presented in the same paper. It allows to find migration route and/or breeding area of a population which migrates to a winter-quarter with a very low detectability of ringed birds, while other populations winter in the areas characterized by a good detectability. The necessary raw data are very simple - they are represented by a number of ringed birds per breeding area, per ringing station or the wave of migrants and number of recoveries in the same division. The low recovery rate (or in other words - high number of ringed birds per one recovery) shows the recruitment area and the route of migration of the population studied. The Figure 7 demonstrates the result obtained in such an analysis of Song Thrush migration.

The other stream of the new methods of quantitative presentation of long-distance recovery data bases on calculation of mean geographical position of recoveries by months. This is a very spectacular mode of synthetical illustration, but on condition of homogeneity of the studied group. This condition is relatively well observed in the example presented in the Figure 8. Both

Fig. 8. Mean coordinates of recoveries of Ospreys during their first autumn flight from Scandinavia and Finland respectively. Roman figures denote month of recovery; arabic figures indicate number of recoveries included in the calculations. After Österlöv (1977)



distinguished populations are not completely separated, but the general picture seems to be right.

Retraps and direct recoveries data studied in the net of collaborating stations can give very valuable results. Here is an example.

The 1974 year irruption of Coal Tit was studied by the net of east and south Baltic ringing stations. Altogether there were ringed 35 991 individuals and 1205 direct-recoveries were obtained. Although migration dynamics was hard to evaluate on the basis of waveness analysis, the study of migration speed at subsequent stages of the route allowed to determine probable population structure of migration (Fig. 9) and pointed out some facts confirming existence of interpopulational isolation mechanisms. The same direct-recovery data, but in the form of direct-recovery rates formed the basis for calculation of income and outcome budget of migrants stream at different stages of migration. This will be presented more extensively in the lecture at irruptive bird symposium on the last day of the Congress.

It is worth stressing that in all these methods, with one exception of calculation of mean co-ordinates, the recoveries were used with ringing and/or seasonal migration dynamics data together.

The special attention should be given to the methods of biometrical analysis. This is a relatively new discipline of bird migration studies. The main obstacles of its development are of double nature. Firstly, technical and

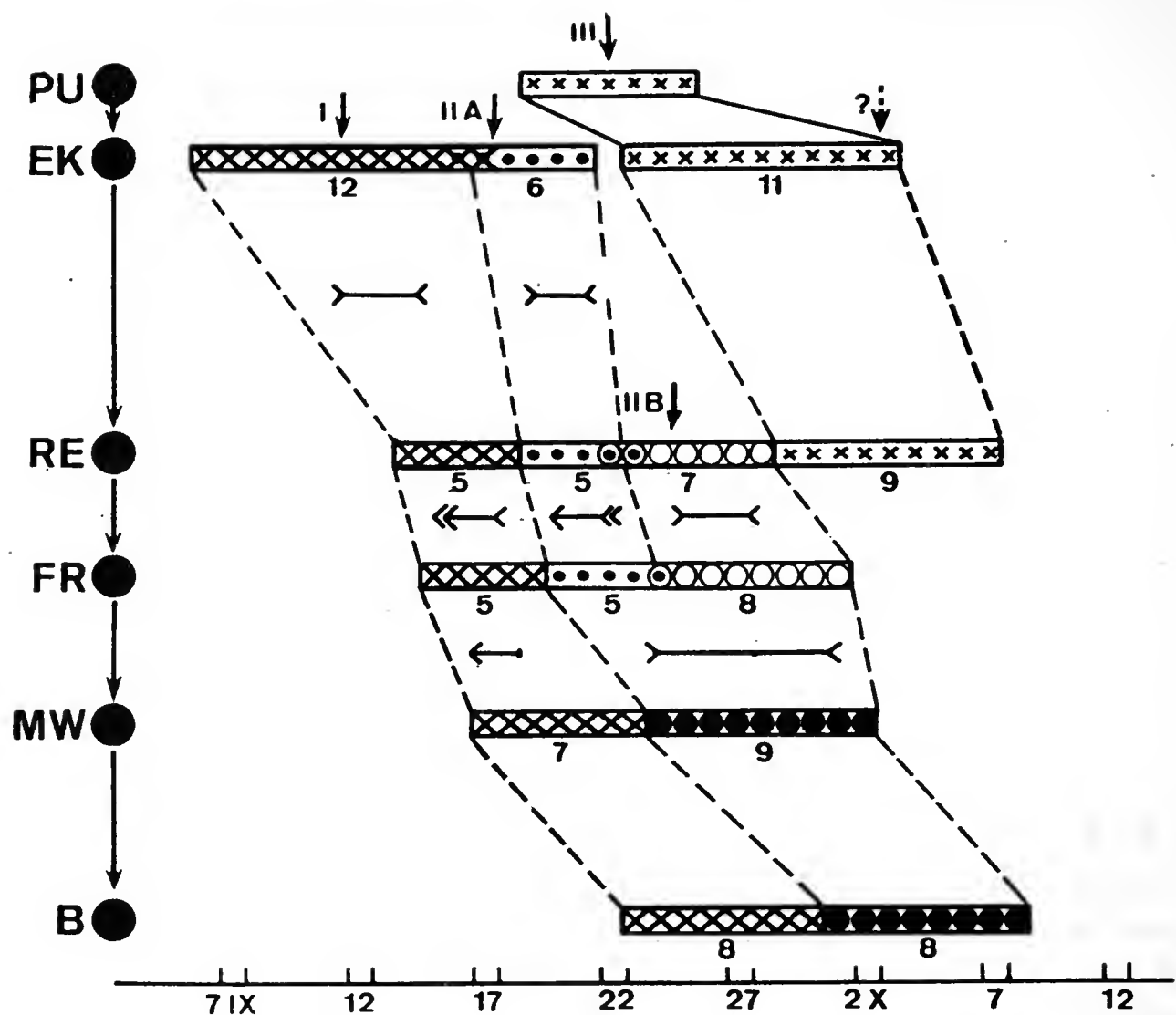


Fig. 9. Scheme of Coal Tit autumn migration 1974. Groups differentiated by signs used; small vertical arrows - points of coming in of bird group into studied migration route. Number of days occupied by passing group is given. Symbols of bird stations: PU - Puise, EK - Kabli (Estonian SSR), RE - "Regulus" (Latvian SSR), FR - "Fringilla" (Russian SFSR), MW - Mierzeja Wiślana, B - Bukowo (Poland). After Busse (1978)

organizational limitations of the collecting of data in the field: more advanced analyses need mass data, whose number should reach sometimes thousands of measured birds. This is because of the statistical requirements. The economical organization of a bird station's work is rather rare and this limits strongly the number of studied birds and the scope of measured parameters. Secondly, there does not exist a clear conception of work. In a number of papers collected biometrical data are presented, but not really analysed. There prevails a very common opinion that one measurement, usually of the wing-length or weight, is fully sufficient for the description of a population. In the most drastic cases of adherence to the Bergman's rule, one notices a tendency to reduce to a straight line all wing-length differences existing in the course of migration. Moreover, there are known attempts to localise the bird group in the map basing on the wing-length measurements only. And this may occur in the situation when the biometrical structure of the species is very complicated and cannot be easily grasped by too simplified methods. In most of the cases the one-parameter biometry leads to the rejection of the selected method of migrational studies.

Collecting of complex biometrical data gives a much wider area for an analysis, than any single parameter study. It is possible to analyse every

parameter separately, but one should also remember about the correlation between different parameters. There is a very common opinion that some parameters are always correlated positively, and correlated to such an extent that one can calculate eg. the tail-length when the wing-length is known. This generalization is completely false. More detailed studies can reveal different possibilities. There are observed even such situations where intrapopulation correlation between the wing and tail lengths or the wing-length and weight is positive, but interpopulation - negative.

The intrapopulation correlation analysis carried out according to the correlation topography method (Busse, 1968) still leaves many questions unanswered at the moment and it will be not discussed more extensively.

Other rising biometrical questions, as the yearly oscillations of biometrical parameters of population, the possible breakdown of the clines at the borders of phylogenetical populations, the probable structure of the singular wave of migrants and others await elucidation. Biometry can be pointed as one of the most promising fields of work for the future migration studies. Although biometrical structure of the species can be, theoretically, studied in the breeding areas, the only economical and effective manner is to study it at migration. Nobody can organize mass measuring of birds on hundreds of thousands square kilometers of breeding grounds.

A similar problem exists in long-term population dynamics studies, which are the youngest stream of migrational research. Breeding bird censuses, although irreplaceable in some aspects, cannot cover with sufficient intensity even the whole territories of the most advanced countries. The only practical solution is to study this problem at migration, when the birds from wide areas pass through a limited area of the bird station. There remain, however, some field work difficulties discussed earlier. Moreover, if the obtained results are to be interpreted both theoretically and practically, the program of research must include identification of recruitment areas and winter-quarters of counted birds. It means, to remind it once more, studying of population differentiation and, once more too, organization of work into the complex program.

Although different populations of the same species can have a differentiated number dynamics, some kind of interspecies synchronization of this dynamics was observed.

The reasons of general synchronization and exceptions from this, similarity of the number dynamics at different areas or its differentiation, these are exciting problems for further studies.

Drawing to a close, I would like to explain why so many methods, I have presented, were born in Poland. Well, the cause lies in the geographical and ecological aspects of migrations of European birds. Europe is an area with the most complicated, in the world scale, bird migration pattern, which is caused by the post-Ice Age history of the continent. In the centre of it, at the intersection of migration routes from the north-east to south-west and from the North to the South and south-east, there is my country - Poland. This localisation is the best one for the work on methodical problems of bird migration. The students of this phenomenon in the regions with a less complicated pattern of the passage or even working at northernmost breeding areas

and at southern winter-quarters could never meet so many situations forcing special methodical studies. These researchers work in the conditions which make the complexity of work far from obvious and the necessity of population studies - still less obvious. But I am deeply convinced, that both - complexity and population differentiation are the key-words of every wider study devoted to the geographical and ecological aspects of bird migration.

SUMMARY

In the lecture there are discussed methodical problems connected with some geographical and ecological aspects of bird migration (distribution, population differentiation, seasonal dynamics, long-term dynamics). These problems are on three levels of scientific work: collecting of raw data, storage, exchange and technical manipulation of the material, the analysis. They are both of substantial and technical ones.

The problems discussed more extensively are as follows: (1) suspending of some species ringing, (2) quantitative catching, (3) organization of station work and complexity of studies, (4) exchangeability of data, (5) presentation of ringing data, (6) populations differentiation. There are presented, with examples, some new analytical methods: (1) waveness analysis, (2) quantitative treatment of ringing recoveries (quantitative distribution of ringed birds, recovery rate analysis, calculation of mean geographical co-ordinates, analysis of direct-recoveries), (3) many parameter biometrical analysis, (4) long-term number dynamics.

There are proposed two key-words of discussed problems. They are as follows: "Complexity" and "Populations differentiation".

Close of the lecture presents the reasons, why methodical problems are intensively studied in the Central Europe.

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RECENT RESEARCH ON TITMICE IN NORWAY

Svein Haftorn

University of Trondheim, Royal Norwegian Society of Sciences and Letters, the Museum, Erling Skakkesgt, Norway

The first part of the paper concerns egg-laying and incubation behaviour, regulation of clutch size and the energetic cost of incubation. I intend to bring the paper to a close by summarizing the results on hypothermia and metabolism in sleeping tits during winter nights.

The studies described here were all carried out in Central Norway, at approximately 63°N. Those on breeding biology took place at a small field station south of the university town of Trondheim. This field station is equipped with such modern facilities for field studies as closed-circuit television and data-loggers.

Before going into the problems, I would like to remind the reader of the following facts. Only the female titmouse incubates. The eggs are laid in the early morning, on consecutive days. Effective incubation starts already during the egg-laying period and develops gradually (Haftorn, 1966, 1981a). This pattern is combined with the female's nightly stay in the nest (Fig. 1). When the female enters the nest in the evening, she immediately removes the nesting material which usually covers the eggs during the daytime. Then she sits down in a normal incubation posture. In consequence, the temperature of the eggs increases abruptly. During the first part of egg-laying period, however, the female incubates for a short time only. After a while she stands up and spends the rest of the night standing in the nest cavity, in the usual sleeping posture. Since there is now no direct contact between the brood patch and the eggs, egg temperature declines. Just before the female leaves the nest the next morning, a slight peak in the egg temperature curve marks the time at which a new egg was laid. Thereafter she covers the eggs with nesting material and departs. The nightly incubation time increases more or less regularly throughout the egg-laying period and during the final few nights the female incubates continuously all night (Fig. 2).

Daytime incubation also develops gradually. It starts later on during the egg-laying period, and is usually not fully developed until the clutch is complete, or even later (Haftorn, 1966, 1981b).

The clutch size varies both between and within the species. In the Great Tit it thus usually ranges between 6 and 12 eggs. There is a seasonal decline in clutch size, a tendency which for example in the Great Tit (*Parus major*) has been recorded in all the populations so far studied (e.g., Czechoslovakia, Balat, 1970; Holland, Kluyver, 1951; Balen, 1973; England, Lack, 1955, 1958; Perrins, 1965, 1979; Finland, Haartman, 1969; Norway, Haftorn, 1981a).

Now a few words about the development and efficiency of the brood patch during the egg-laying period. The maximum temperature attained in the eggs during the nightly continuous incubation in the egg-laying period may provide a useful indication of the stage of development of the brood patch. Since the nightly maximum egg temperature recorded increases progressively throughout the egg-laying period, there is a reason to believe that this is due to an in-

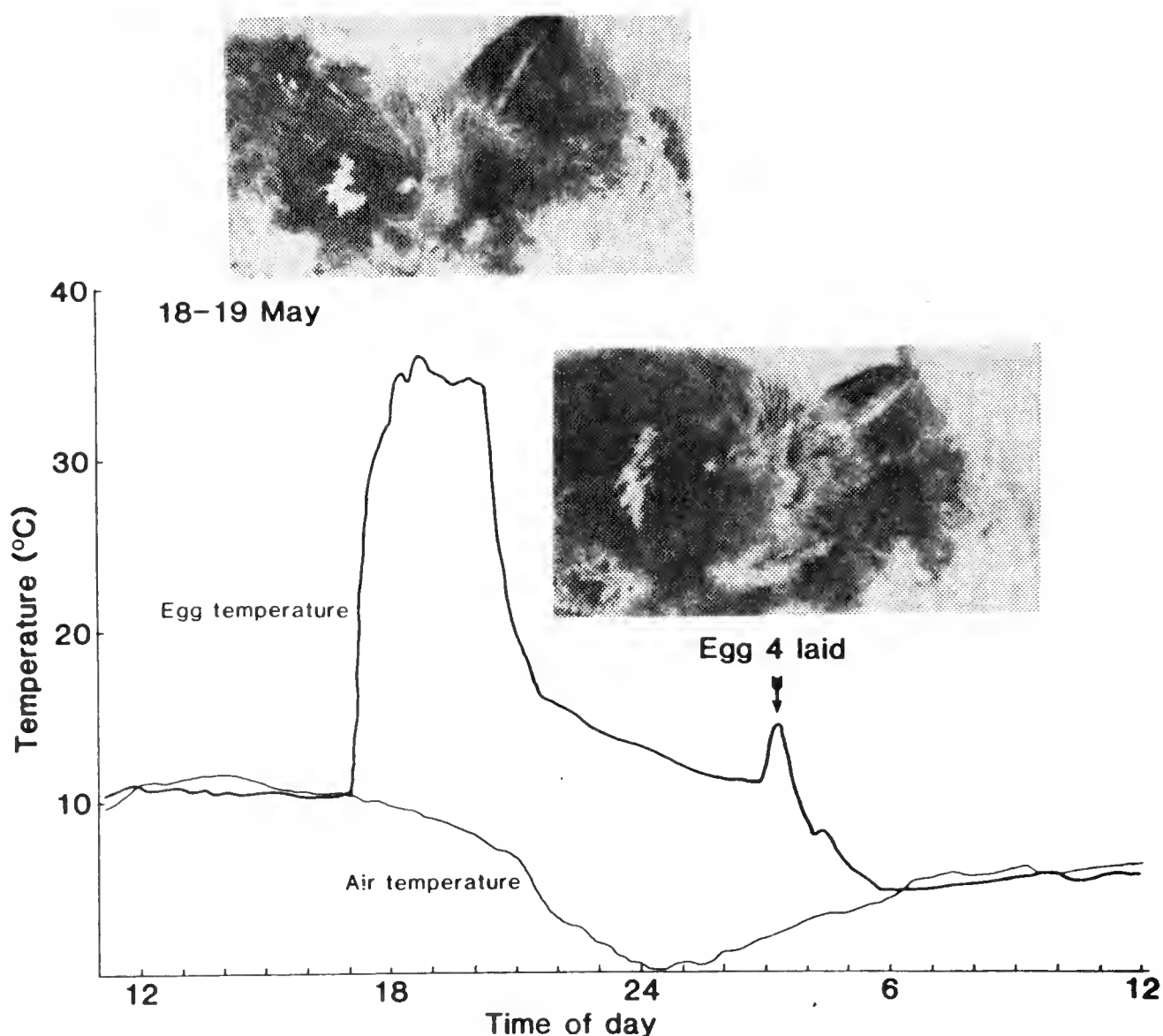
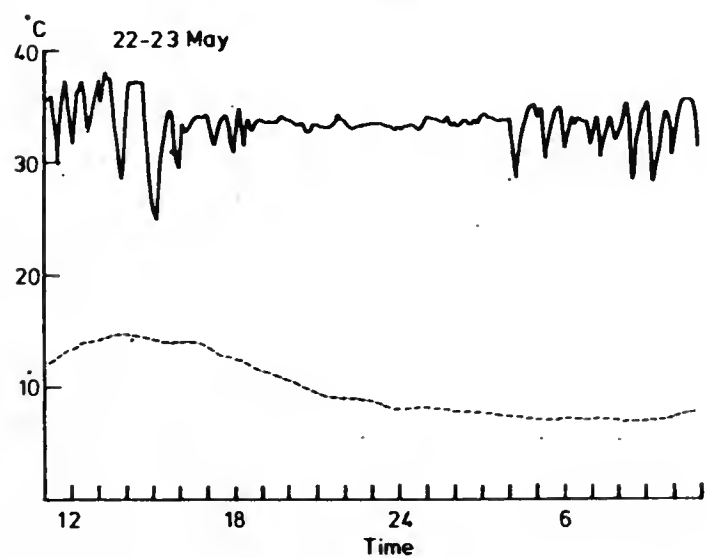
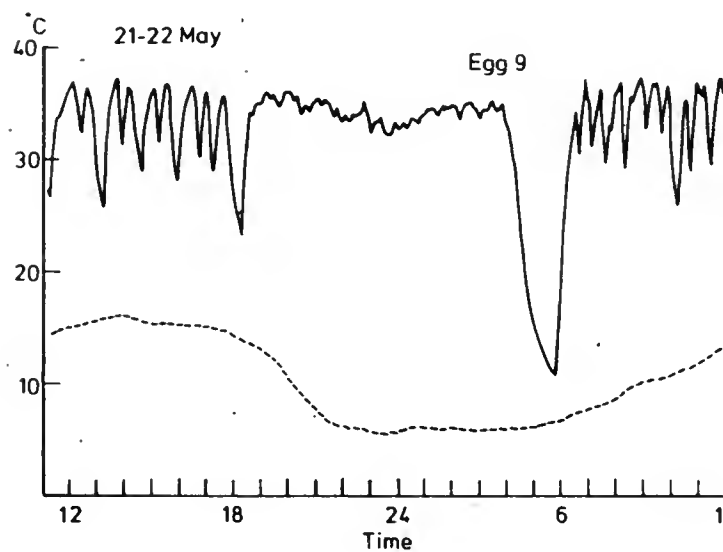
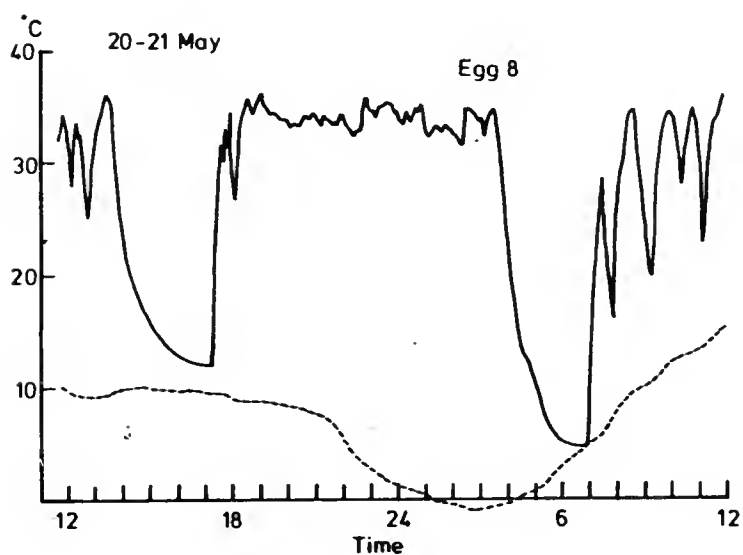
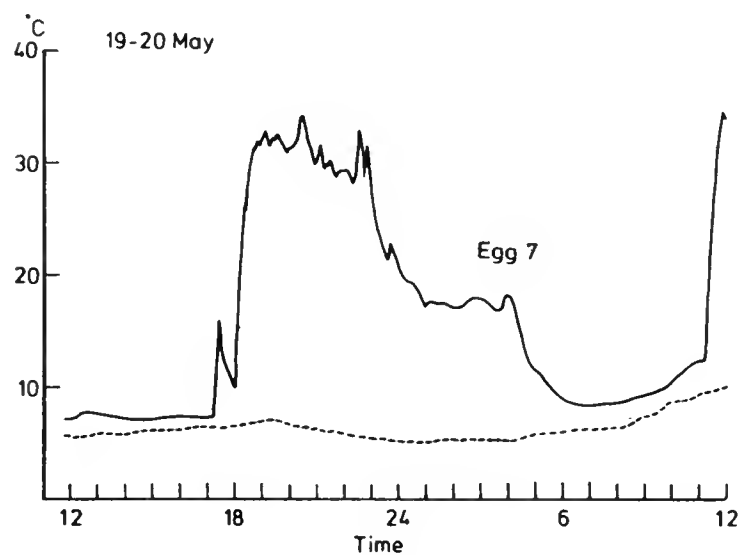
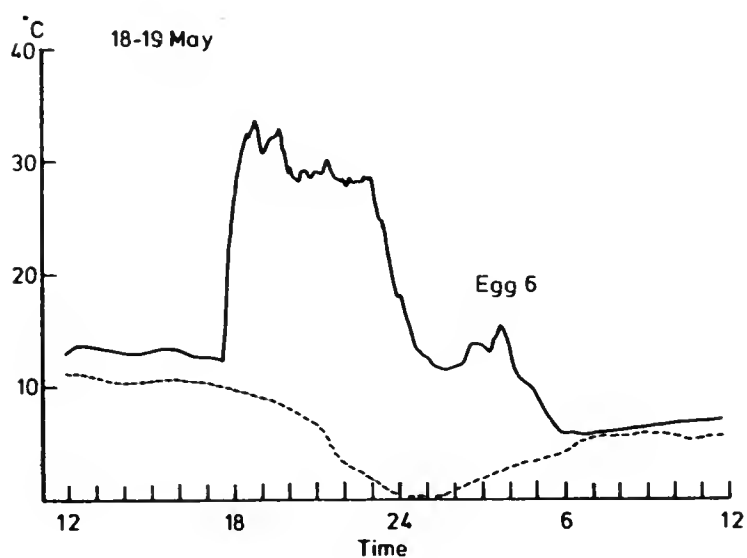
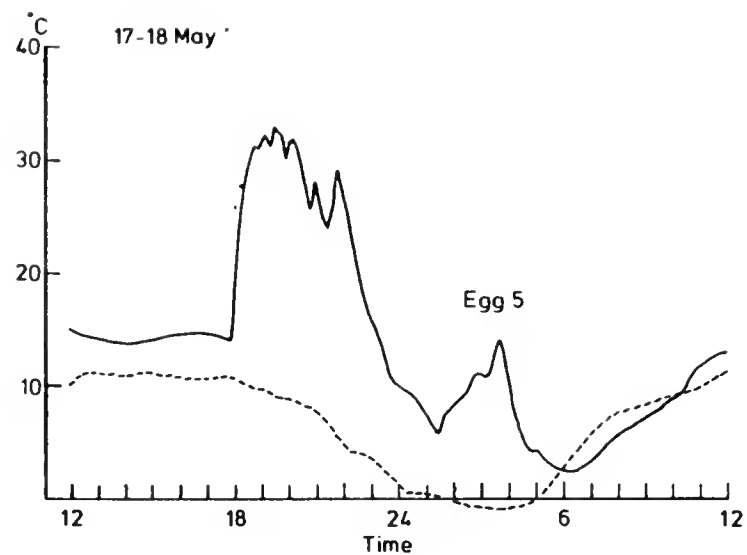
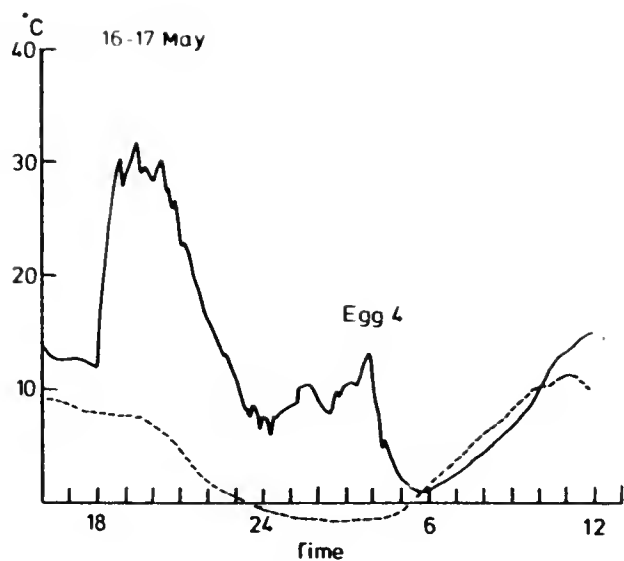


Fig. 1. Typical pattern of egg temperature during the early part of the egg-laying period in a tit nest. The photographs show the female (Coal Tit *Parus ater*) in normal incubation posture (high egg temperature) and standing in the nest cup without incubating (decreasing egg temperature)

crease in the efficiency of the brood patch, and that this is not fully developed until the clutch is complete, although the female's abdomen has become featherless long before that particular day (Haftorn, 1981a). Nevertheless, already at the beginning of the egg-laying period the incubating female is capable of raising the egg temperature above the threshold for embryonic development. This is considered to be about 25°C. Because of effectiveness of incubation during the egg-laying period, the eggs do hatch more or less *asynchronously*, usually within a period of three days. As would be expected, the length of the hatching period which is the time from the first- to the last-hatched young, is significantly correlated with the incubation effort during the egg-laying period (Haftorn, 1981a).

In discussing the causal problems of clutch size in tits, Perrins (1979) stated that the "mechanisms by which the birds adjust their clutch size is not known at all". This statement is certainly close to the truth, although we now know that quite a few factors do correlate with clutch size. For example, the age of the female, breeding density, laying date, and type of habitat (Kluyver, 1951; Perrins, 1965; Haartman, 1969; Dhondt in Balen, 1973; Balen, 1973). Even the size of the nest chamber may influence the clutch size, inasmuch as smaller clutches are laid in small nest chambers than in large ones (Löhr, 1973; Ludescher, 1973; Karlsson and Nilsson, 1977). However, the causal effect of



F i g. 2. Egg temperature (upper curve) and the air temperature outside the nest (lower curve) during the egg-laying period (after laying of the third egg) and the first day of the incubation period at a Great Tit Parus major nest (clutch 9 eggs). After Haftorn (1981a)

all these factors has recently been questioned by van Noordwijk et al. (1981), who claim that about 40% of the phenotypic variation in clutch size is in fact genetic variation.

To the above factors, all of which are somehow related to clutch size, at least one more factor can be added, namely the rate of incubation development during the egg-laying period. In a study of the Great Tit this rate of incubation development was shown to be inversely correlated to clutch size (Haftorn, 1981a). This relationship holds true even when the seasonal decline in clutch size is taken into account. The faster the incubation pattern develops in any particular nest, the fewer is the number of eggs which will be laid in that nest (Fig. 3).

How the clutch size of tits is determined is far from being clarified, but on the presently available evidence the following speculations are permissible.

As known from the pioneer work of the Dutch ornithologist, the late Dr. Kluyver (1952), in early spring the ovarian follicles of tits increase in size very slowly at first, but just before the laying period the ovary starts to swell considerably. From the start of this period of rapid growth up to the laying of the first egg about 4 days elapse.

Daily egg-laying is ensured by the successive development of egg follicles. This implies that at the moment the first egg is laid, three other follicles are at different stages of rapid growth and a fourth follicle is about to start its rapid development (Fig. 4). This situation is then repeated every day until three days before the last egg of the clutch is to be laid. At this point in time the fourth follicle degenerates, instead of developing further.

The crucial question is thus: which factor or factors decide the fate of this fourth follicle, whether it shall continue to develop further, or degenerate?

There is no reason to believe that external factors as for example the air temperature, are decisive. The air temperature does indeed exert a marked influence on the timing of the start of egg-laying (Kluyver, 1951, 1952; Lack, 1958; and others), but so far there is no indication that air temperature also affects the termination of egg-laying and thereby the clutch size. The presumption that the air temperature prevailing at the time when the final, rapid follicle development of the last egg starts, in other words about four days before egg-laying ceases altogether, has thus not been confirmed (see Haftorn, 1981a). This result is by no means surprising, because a more detailed investigation of the above-mentioned relationship between clutch size and incubation rate during the egg-laying period strongly indicates that the mechanisms responsible for regulating clutch size are already operative at the start of the egg-laying period, perhaps even earlier.

This view is based on the fact that a significant correlation between clutch size and the daily incubation rate was found already after the second egg was laid (Table 1).

Because of the close relationship which exists between the incubation rate and clutch size, it is reasonable to suppose that the incubation rate either has a direct effect on clutch size, or is linked to other factors which have such an effect.

If we for clutches of various size calculate the total daily time which the

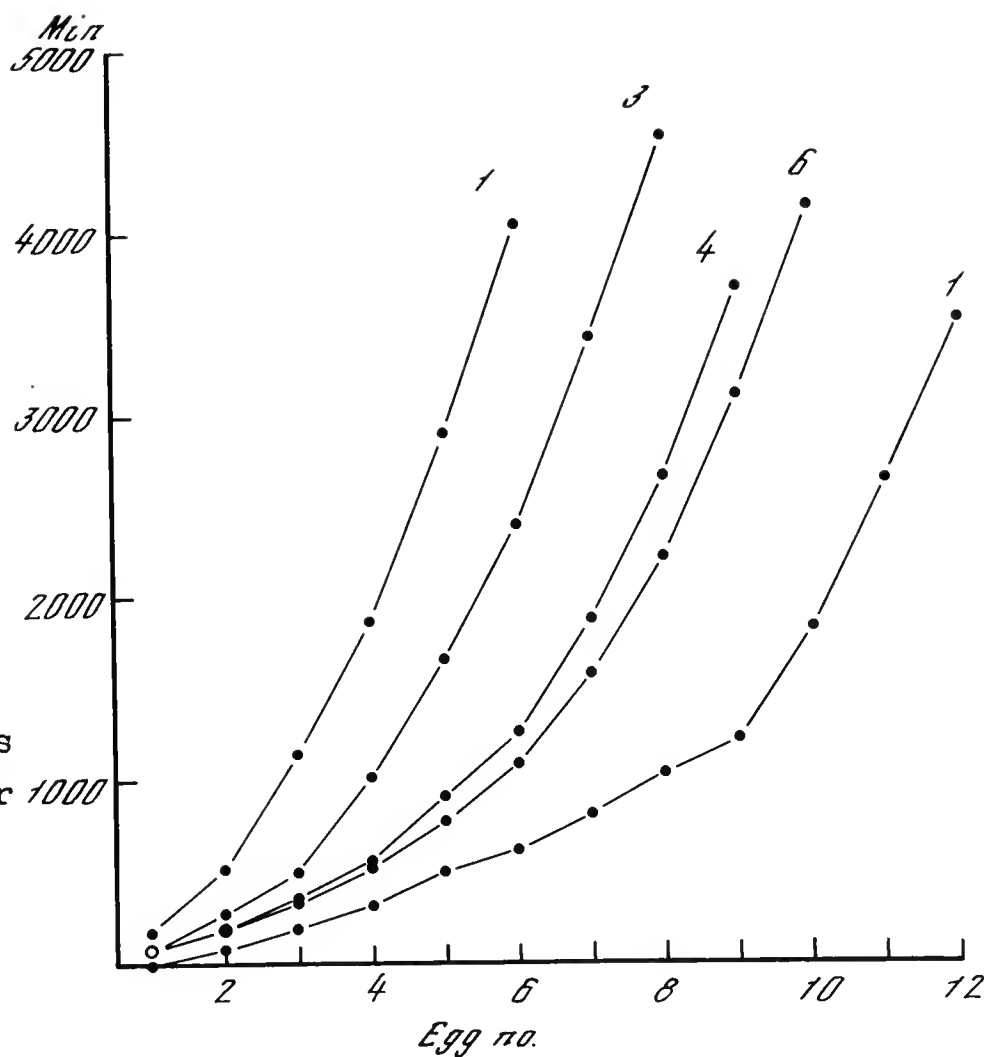


Fig. 3.
Cumulative total of incubation
(in minutes) for the 24-h periods
after each egg had been laid, for
Great Tit clutches of 6-12 eggs.
Numerals indicate the number of
nests on which the curves are
based. After Haftorn (1981a)

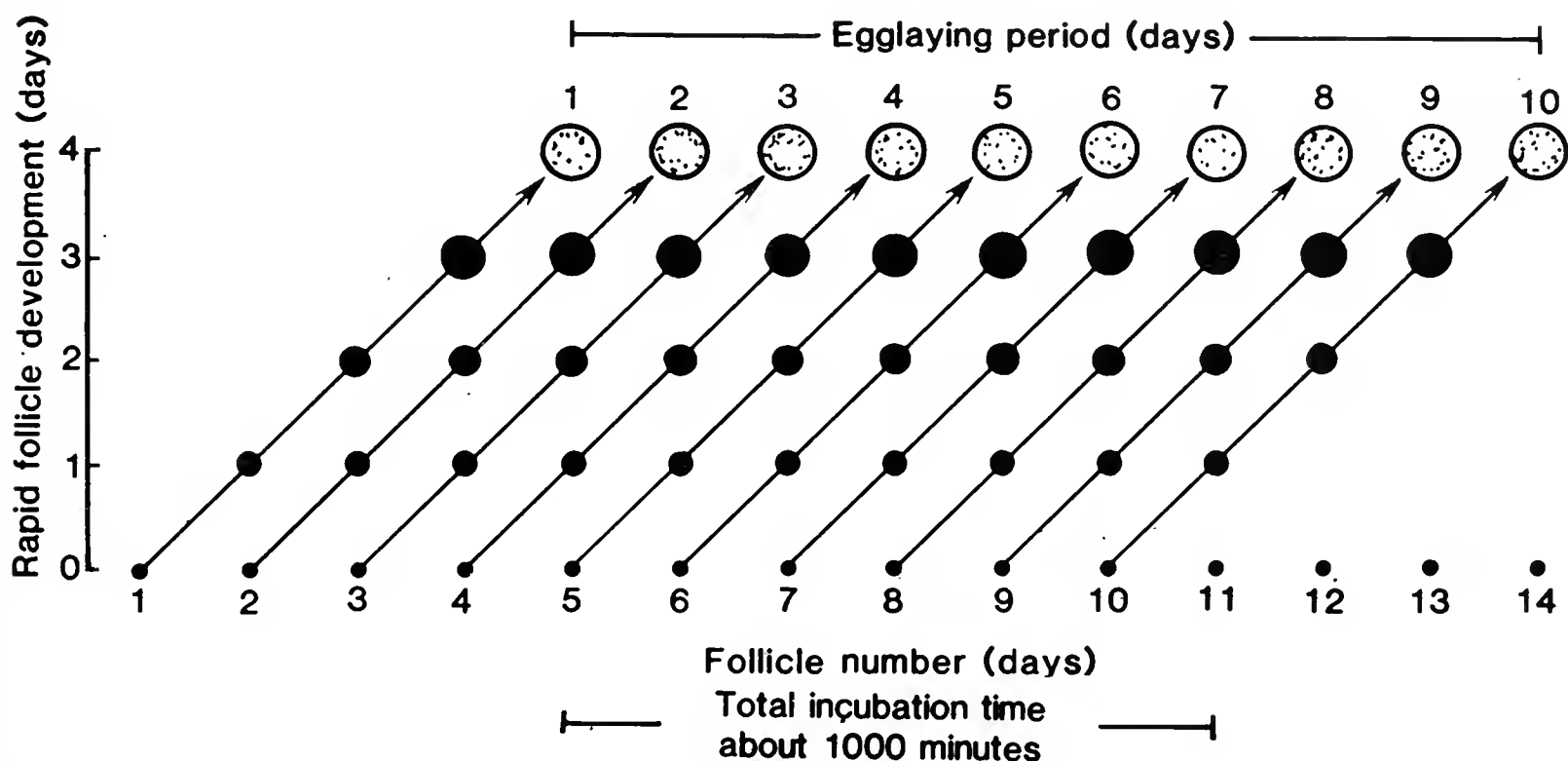


Fig. 4. Schedule of follicle development from start of the rapid growth
phase of the first egg to the last egg has been laid in a clutch of 10 eggs

female has spent incubating, from the time the first egg was laid, until three days before the last egg was laid, i.e. the point at which the egg follicles are supposed to degenerate instead of entering into the phase of rapid development, the result is a total incubation time of about one thousand minutes (Fig. 4), a rather thought-provoking finding. It seems to me that a certain incubation effort is required to induce further egg-laying to stop.

T a b l e 1. The Pearson correlation coefficients obtained for the relationship between incubation time, clutch size, duration of hatching period and time (laying date). Inc. 2 (Inc. 3 etc.) represents the duration of incubation during the 24-h period after the second (resp. third egg etc.) was laid. The table is based on 15 nests of the Great Tit(Parus major). After Haftorn (1981a)

| | Time | Inc. 2 | Inc. 3 | Inc.4 | Inc. 5 | Hatch. per. |
|--------|----------------|------------------|------------------|------------------|-----------------|----------------|
| Clutch | -0.58* (15) | -0.80*** (14) | -0.78*** (15) | -0.82*** (15) | -0.88 (15) | -0.38 (11.) |
| Time | | 0.59* (14) | 0.74*** (15) | 0.71** (15) | 0.61* (15) | 0.55 (11) |
| Inc. 2 | | | 0.85*** (14) | 0.86*** (14) | 0.88*** (14) | 0.66* (11) |
| Inc. 3 | | | | 0.83*** (15) | 0.85*** (15) | 0.38 (11) |
| Inc. 4 | | | | | 0.91*** (15) | 0.61* (11) |
| Inc. 5 | | | | | | 0.58 (11) |

That incubation may inhibit the growth of the follicles and cause them to degenerate has been proven experimentally in gulls (Paludan, 1951; Weidmann, 1956). Several gull species normally lay three eggs. If, however, the incubation contact of the female with the first egg is prevented, ovarian follicle N 4 starts to develop instead of degenerating, and she lays a clutch of four eggs instead of three.

In such matters, of course, it is difficult to distinguish between cause and effect. In other words, whether clutch size is influenced by the incubation behaviour, or whether the incubation effort is adjusted to an anticipated number of eggs. At present I am inclined to favour the hypothesis that incubation per se has a feedback effect on the endocrine state of the female. If for example, the level of follicle stimulating hormone (FSH) is lowered, then egg production will cease when this level has fallen below a certain critical threshold value. The incubation rate itself may depend on how quickly the levels of the relevant hormones change with time. Slow changes of hormonal levels from day to day during the egg laying period would result in a low incubation rate and consequently in a slow approach towards the point at which follicle development in the ovary becomes depressed (Fig. 5). This possible pattern of development corresponds to the situation seen in the early spring, when the Great Tit lays relatively large clutches.

This hypothesis implies that the mean rate of change in hormonal levels increases throughout the breeding season, and thus explains the observed seasonal decline in clutch size.

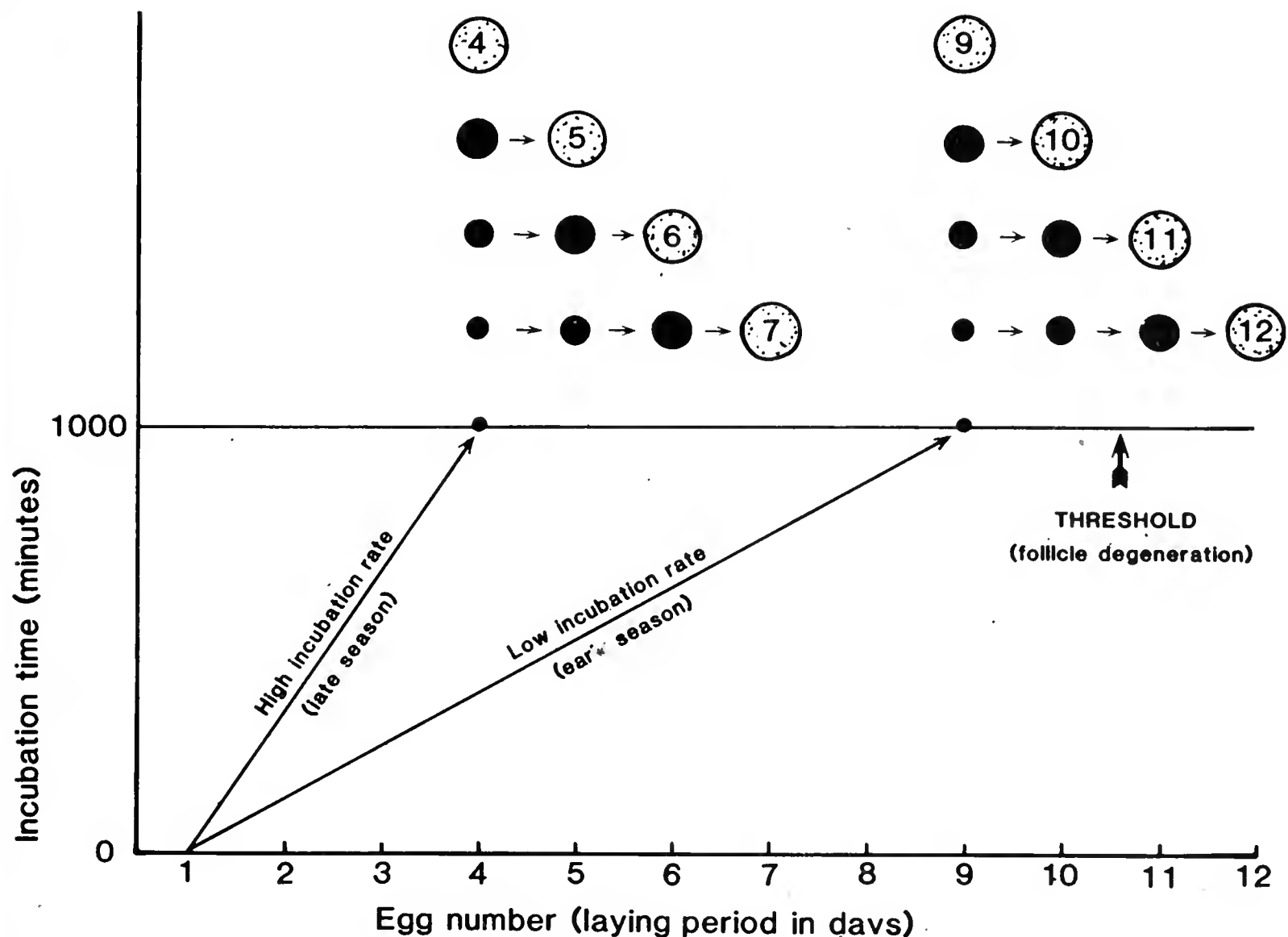


Fig. 5. Possible feedback effect of the female's incubation effort (in the egg-laying period) on termination of egg-laying. The clutch size may depend on the incubation rate. Clutches of 7 and 12 eggs, respectively, exemplified in the model

This view is highly speculative, of course. The determination of clutch size is undoubtedly a very complex procedure. Nevertheless, considering the high proportion of variation in clutch size, which according to statistical analyses is accounted for by the incubation factor alone, namely roughly 75% in the Great Tit (Haftorn, 1981a), my opinion is that the amount of incubation during the egg-laying period should be taken thoroughly into account in future studies of clutch size determination.

Turning now to the incubation period of titmice, in other words the period from the time the last egg has been laid to the time of hatching of that egg, we face the problem as to how the female is able to maintain a mean egg temperature of about 36°C throughout the incubation period, regardless of changes in the ambient air temperature. Extensive research has shown that the female partly solves this task by regulating the time she spends sitting on the eggs (Fig. 6). Thus, with increasing ambient temperature, the mean duration of the incubation bouts, or periods-on, declines, at the same time as the periods spent off the eggs tends to increase (Haftorn, 1973, 1979, 1981b). Consequently, the total daily attentive time declines with the increase in air temperature. If we look at the situation during the daytime, it is quite clear that the daily minimum of attentiveness coincides with the daily maximum of air temperature (Fig. 7). However, the correlation coefficients between attentiveness and air temperature are, after all, only relatively moderate, and

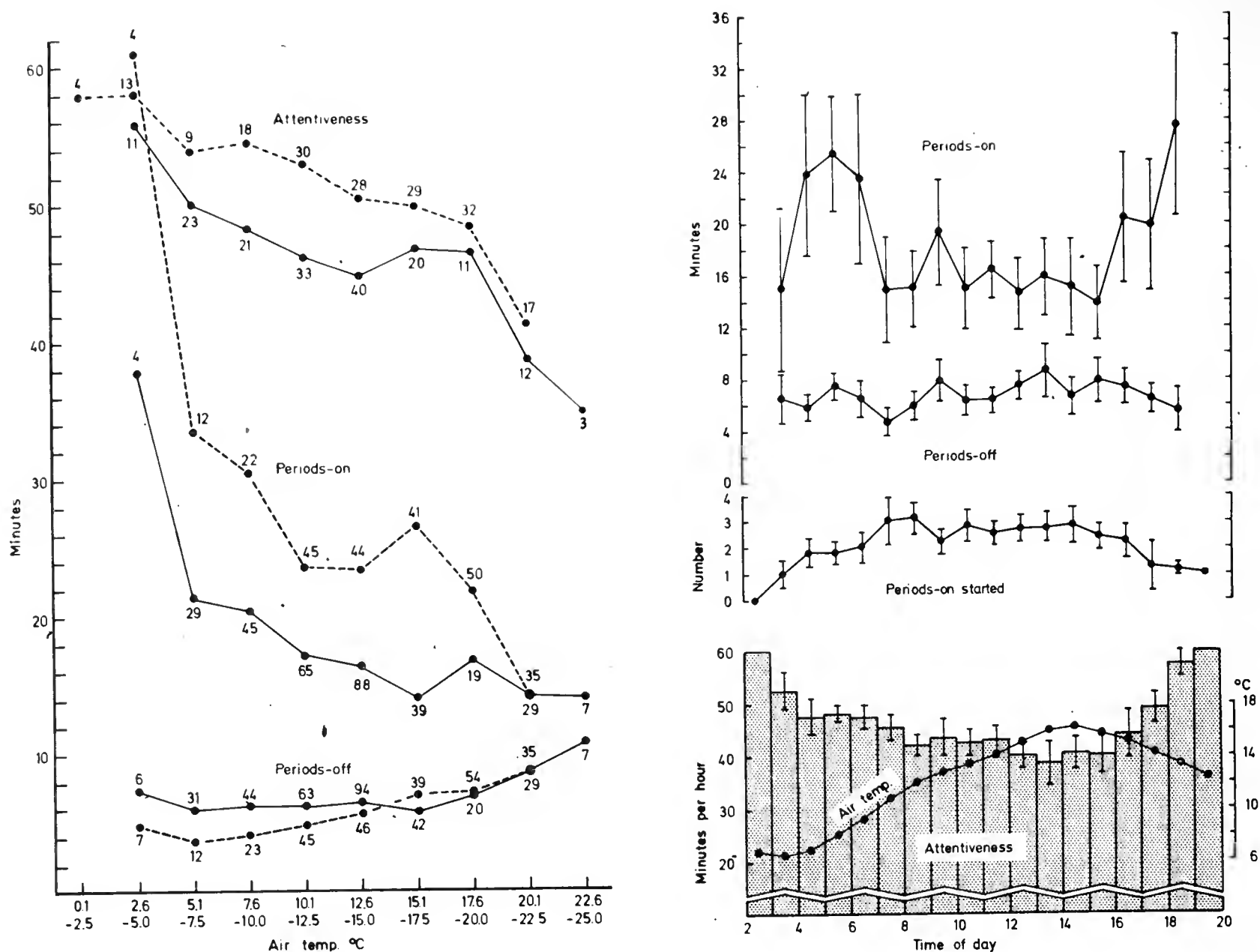


Fig. 6. The relationship between air temperature and incubation rhythm in two nests of the Willow Tit *Parus montanus*, based on the mean values of periods-on, periods-off and attentiveness within the respective temperature intervals indicated. Numerals along the curves denote the number of periods-on and periods-off; solid lines - nest 1/73, dashed lines - nest 1/74; for attentiveness the numerals indicate the number of hours of observation. After Haftorn (1979)

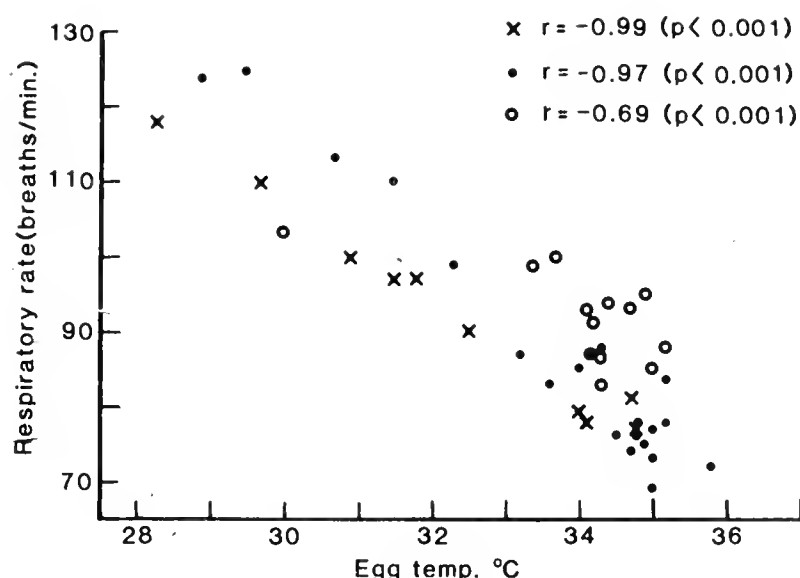
Fig. 7. Duration of hourly means ($\pm 2SE$) for periods-on, periods-off and attentiveness at a nest of the Willow Tit, together with the number of periods-on started, and the mean air temperature. After Haftorn (1979)

this indicates that a substantial part of the variation in attentiveness remains which cannot be explained by the air temperature alone. Thus, when the impact of air temperature on attentiveness was excluded in partial correlation analyses, there was still a tendency for attentiveness to decrease towards noon, and increase afterwards, although this relationship was not consistent (Haftorn, 1979, 1981b). This pattern is possibly linked to the diurnal rhythm of body temperature of the incubating female, which attains its daily maximum just around noon (Haftorn, Reinertsen, 1982).

I mentioned that the incubation egg temperature was about 36°C . Thus, based on a total of about 14 000 recordings, the overall mean egg temperature for the Willow Tit (*Parus montanus*) was 36.4°C during the period of full incubation

Fig. 8.

The relationship between egg temperature and respiratory rate during incubation by the Great Tit. After Haftorn, Reinertsen (1982).



(Haftorn, 1979). This temperature value corresponds to the mean heat applied to the early embryos. Although the female titmouse spends about 20-30% of the daytime outside the nest, she manages to keep the overall mean egg temperature during daytime close to the mean egg temperature recorded during the night, when she incubates continuously. In the Willow Tit I thus found a mean temperature difference of only 0.45°C between day and night.

Now, egg temperature is of course dependent on heat production by the incubating female, and this matter of fact leads me to discuss the relationship between heat production and egg temperature. Besides varying the duration of her attentiveness, and possibly also the tightness of sit (White, Kinney, 1974), the incubating female may, of course, also regulate the egg temperature by varying the amount of heat transferred through the brood patch. The data so far available do in fact indicate strongly that this is precisely what she does. Thus, in the Great Tit a highly significant correlation was found between the respiratory rate and the recorded egg temperature (Fig. 8). Furthermore, when the Great Tit female sat down on artificially cooled eggs, her body temperature - as recorded telemetrically - dropped abruptly at the same time as her respiratory rate went up (Fig. 9). It is noteworthy that, even in experiments in which the eggs were artificially cooled down nearly to freezing, the female was still able to compensate for the heat loss to the eggs within 3-4 minutes, and thereafter produced sufficient energy to increase the temperature of both the eggs and her own body simultaneously. Additional investigations have shown that, during the latter part of typical periods-on, both the body temperature of the sitting female and the egg temperature become stabilized, as also her respiratory rate, indicating that the heat production by the female and the heat loss to the eggs and the environment are by then in balance (Fig. 10, see also Fig. 9).

Having achieved this state of homeostasis during incubation, the female, so to speak, feels satisfied with the situation and changes her behaviour pattern by incorporating a new form of activity. In addition to settling, re-settling and head-down activities including tremble-thrust movements and egg-shifting, she now starts nibbling with her bill on the nest edge (see Figs. 9-10). I interpret this nibbling behaviour, which is typical for all the tit species so far studied, as intention movements to covering the eggs with nesting material. However, a genuine covering of the eggs is solely carried out during the egg-laying period and is never actually accomplished once the clutch is complete. Nevertheless, such nibbling behaviour is a strong indication that

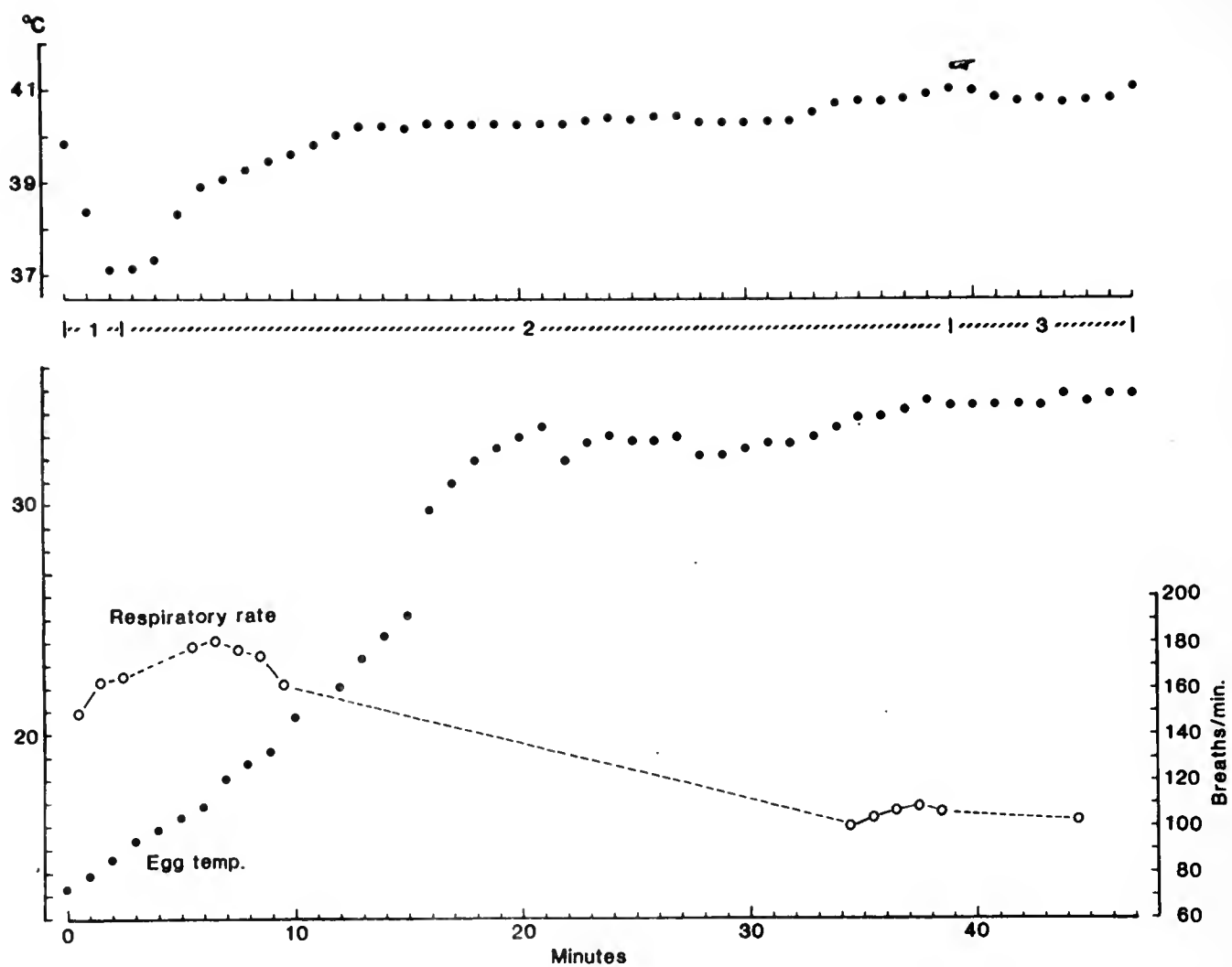


Fig. 9. Body temperature and respiratory rate of an incubating Great Tit female together with egg temperature during a period-on lasting 47 minutes. The eggs were artificially cooled down just before the female entered nest. The hand-symbol indicates start of period with persistant bill-pressing and bill-pulling on the nest edge. Note that different scales are used for body temperature and egg temperature. After Haftorn, Reinertsen (1982)

the incubating female has stabilized both the egg temperature as well as her own body temperature and that she is now ready to leave the nest for a new bout of foraging.

To sum up, we can conclude, from the available information, that the incubating female maintains an optimal mean egg temperature of about 36°C by a combined effect of regulating the duration of attentive time and of heat transfer to the eggs, possibly also by adjusting the tightness of sit. It seems that the incubating female treats the eggs as though they were a part of her own body (Drent et al., 1970; Drent, 1975), and that her main aim during incubation is to adjust her body temperature to a level corresponding to that of her normal resting standard temperature, at the same time raising the egg temperature to the optimal level for embryonic development. The recorded body temperature of the female Great Tit during daytime incubation thus tended to stabilize at 40.6°C (Haftorn, Reinertsen, 1982), a value which does not differ significantly from the mean standard temperature recorded for the proventriculus of tits, namely 40.3°C (Udvardy, 1955).

It is common knowledge that incubation time is subject to a certain degree of variation. For the Great Tit, for example, incubation time ranges from 13 to 19 days, as defined as the period from the last egg is laid to the hatching of that egg (Haftorn, 1971). This variability is at least partly due to an individual variation in attentiveness from female to female. Thus, the incubat-

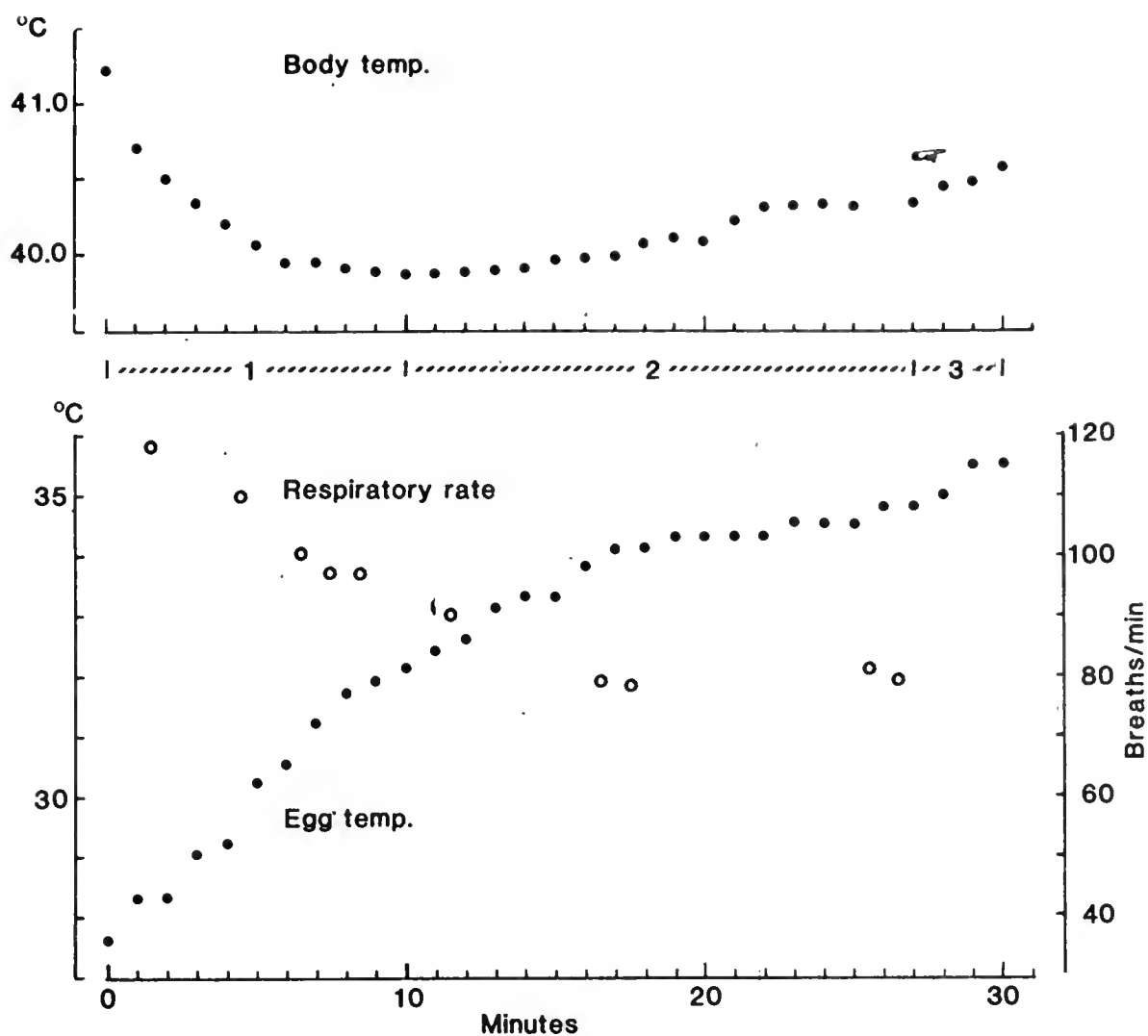


Fig. 10. Body temperature and respiratory rate of an incubating Great Tit female together with egg temperature during a period-on lasting 30 minutes. Note that different scales are used for body temperature and egg temperature. For further explanation see Fig. 9. After Haftorn, Reinertsen (1982)

ion time of the female Great Tit significantly decreased when the mean time spent on the eggs per hour increased from about 60 to 80% (Fig. 11).

The energetic cost of incubation is not easy to measure, and the results have been a subject of controversy among authors. In calculations based on heat-flow models, Walsberg and King (1978) claimed that the resting metabolism of three passerine species averaged about 15-18% below that of non-incubating birds, whereas Biebach (1979) and Vleck (1981), who measured the rate of oxygen consumption, found that, for two other species of passerines, the metabolic rate of the incubating bird lay 20-30% above that of non-incubating birds. Mertens (1980), who measured heat loss from a Great Tit's nest, also found that the cost of incubation was considerable. He used heat-flux disks mounted in the walls of a nest-box occupied by a female Great Tit, and concluded that the heat loss during incubation, at an ambient air temperature of 8°C, was roughly three times greater than the heat loss incurred at the resting metabolic rate.

From an experimental point of view, titmice are ideal birds for evaluating the cost of incubation, as they are for many other types of basic ecological research. They start to spend the night-time in the nest even before egg-laying commences and, as already mentioned, the incubation pattern develops gradually during the egg-laying period. We thus have, outside the laboratory, an excellent possibility to compare the metabolism of free-living individuals,

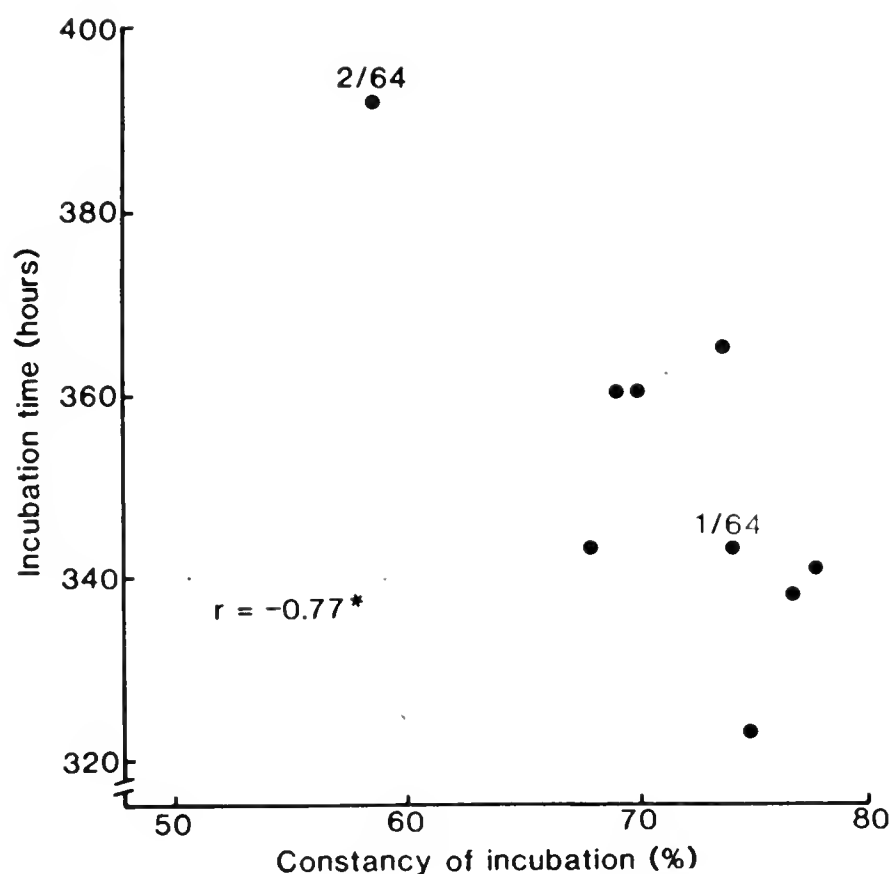


Fig. 11.

The relationship between constancy of incubation and incubation time for nine different clutches of the Great Tit. After Haftorn (1981b)

both during incubation and during non-incubation. In June 1982 we estimated the oxygen consumption of a Blue Tit (*Parus caeruleus*) female, which finally laid a clutch of 10 eggs in a nest-box (Haftorn and Reinertsen, unpublished). Before the experiment was started the original nest-box was replaced by a special box, constructed as a metabolic chamber. During the experiment the entrance hole was closed off by a transparent piece of plexiglass, and air was pulled into the nest through a small hole in the chamber wall, passed the bird, and was let out through a hole on the opposite side. The results of this experiment are shown on Fig. 12. Above an ambient temperature of 16°C, which must be close to the lower critical temperature for this species, the energetic cost of incubation was negligible. Below 16°C, however, as is clear from the figure, the energetic cost was considerable. For example, at an ambient temperature of 8°C, the Blue Tit female increased her resting metabolism by about 40% in order to keep her 10 eggs at an optimal incubation temperature. This experiment therefore lends support to the view that incubation, at least by small-sized birds, requires additional heat to be produced when the ambient temperature falls below the lower critical value of the thermoneutral zone.

How neatly incubating tits compensate for the heat loss due to decreasing ambient temperatures, at least down to freezing point, is illustrated by the fact that the egg temperature remains almost stable (Haftorn, 1979).

Leaving these matters of breeding biology, I will now turn to the problems connected with the conservation and saving of energy by titmice during the winter. At midwinter in Central Norway (about 63°N), tits must build up, during a daylight period lasting only 6 hours, a sufficient reserve of energy to meet their nightly requirement. In other words, the nightly rest in midwinter at these latitudes lasts as long as 18 hours. This long time of diurnal inactivity obviously represents a serious constraint on the birds.

In recent years much attention has been paid, both in Europe and overseas, to the physiology of tits during the winter. The studies so far made have concentrated on three species similar in size, namely the Willow Tit, the Sibe-

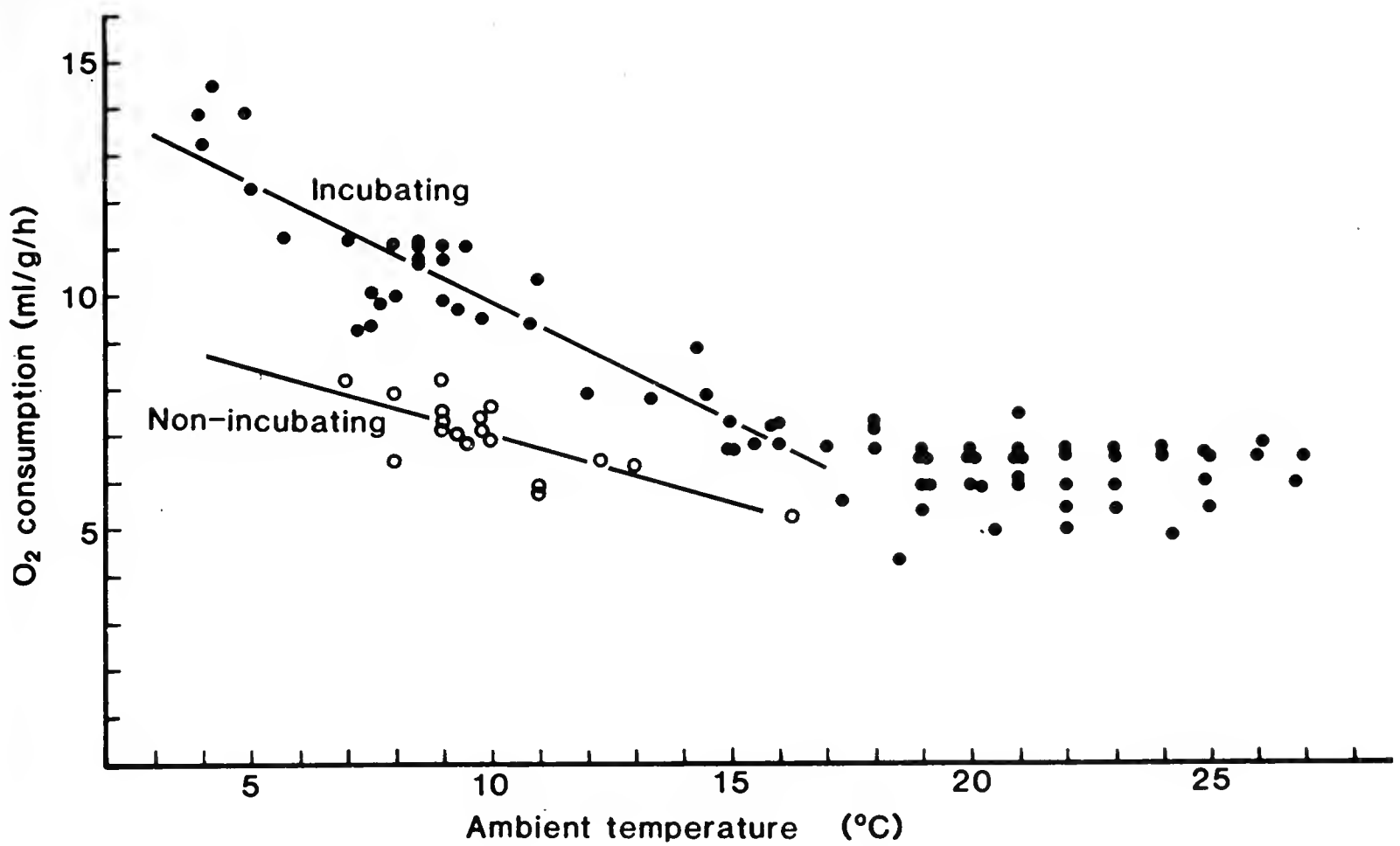


Fig. 12. The relationship between energy metabolism and ambient temperature in a Blue Tit *Parus caeruleus* incubating 10 eggs (closed circles) or standing above the eggs in a resting posture, i.e. not incubating (open circles)

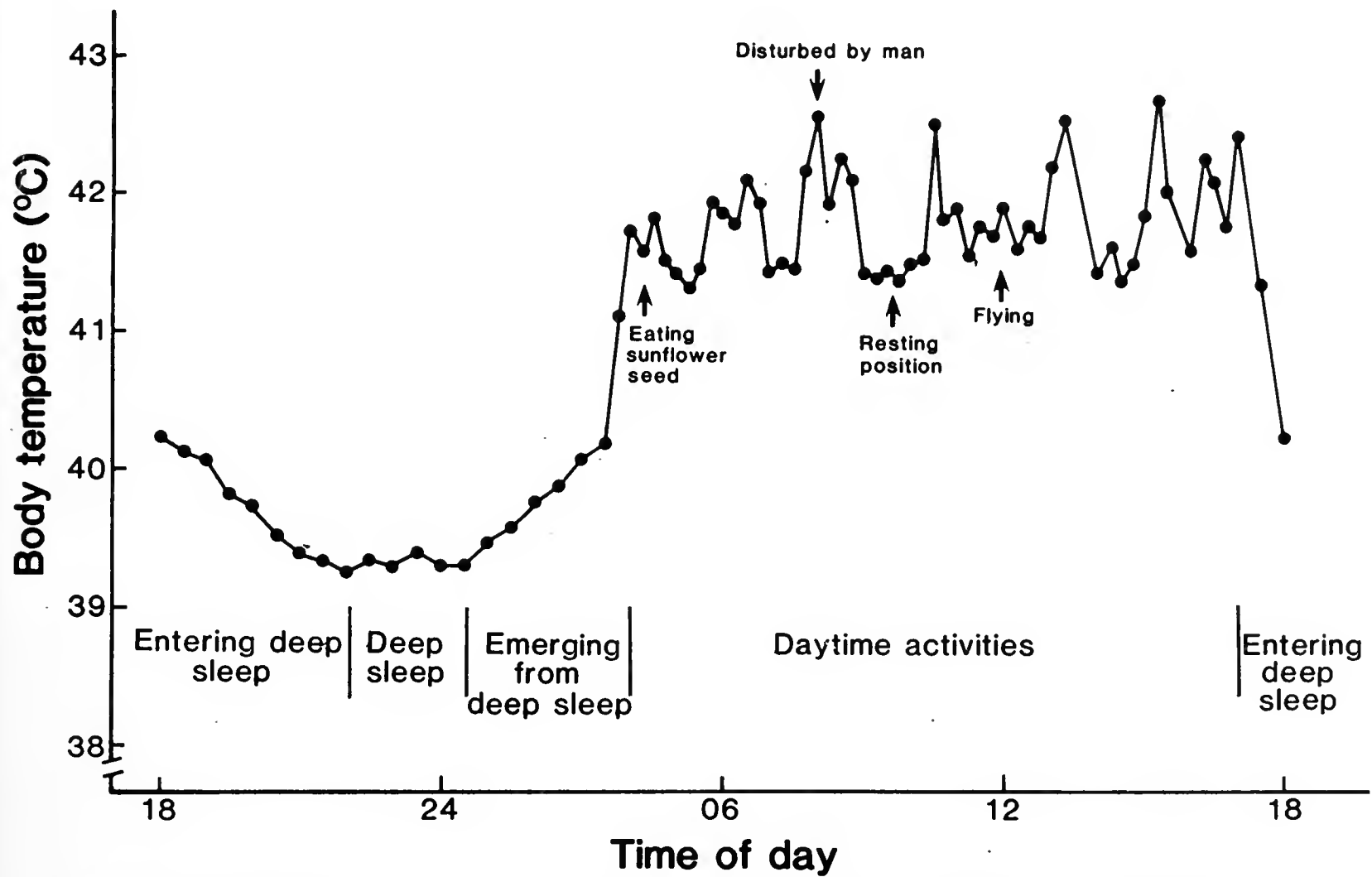


Fig. 13. Circadian body temperature rhythm of a summer-acclimatized Willow Tit. After Reinertsen and Haftorn

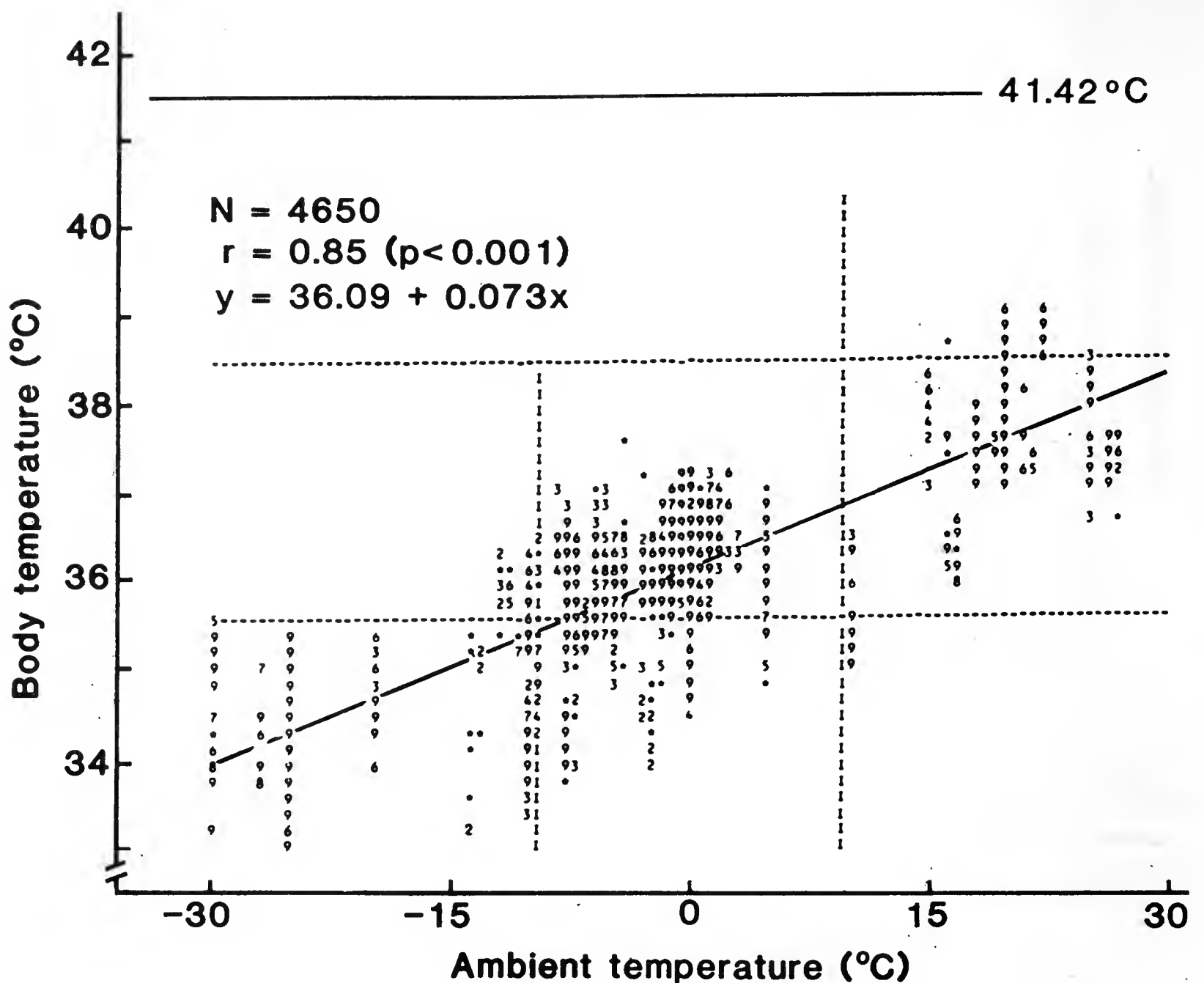


Fig. 14. The relationship between body temperature and ambient temperature, during deep sleep, of winter-acclimatized Willow Tits (10 birds). After Reinertsen and Haftorn

rian Tit (Parus cinctus), and the Black-capped Chickadee (Parus atricapillus).

In Norway an extensive research project on the nocturnal hypothermia and metabolism of the Willow Tit is now in progress (Reinertsen and Haftorn, in press). The body-weight of this bird is only about 12 g. It is noteworthy that the observed nocturnal hypothermia in the Willow Tit and related species during the wintertime involved only a moderate depression of deep body temperature, compared to the torpor observed in Hummingbirds and the Poor-will (Phaenoptilus nuttall). Whereas the body temperature of the latter species may drop to about 10°C during torpor (Bartholomew et al., 1957), that of the tits never seems to fall below 30°C.

In order to get continuous body temperature recordings without disturbing the bird under observation, a small radio-telemetry transmitter, weighing only 0.75 g, was implanted into the intraperitoneal cavity (Reinertsen, 1982). Experimental birds were kept in outdoor cages exposed to the natural climate and in identical cages placed within a constant temperature cabinet, in which they were exposed to controlled photoperiods and ambient temperature regimes.

The diurnal thermoregulation pattern of the Willow Tit was studied at all seasons of the year. In principal, the pattern was found to be the same regardless of season (Fig. 13). From daytime body temperature of about 41°C

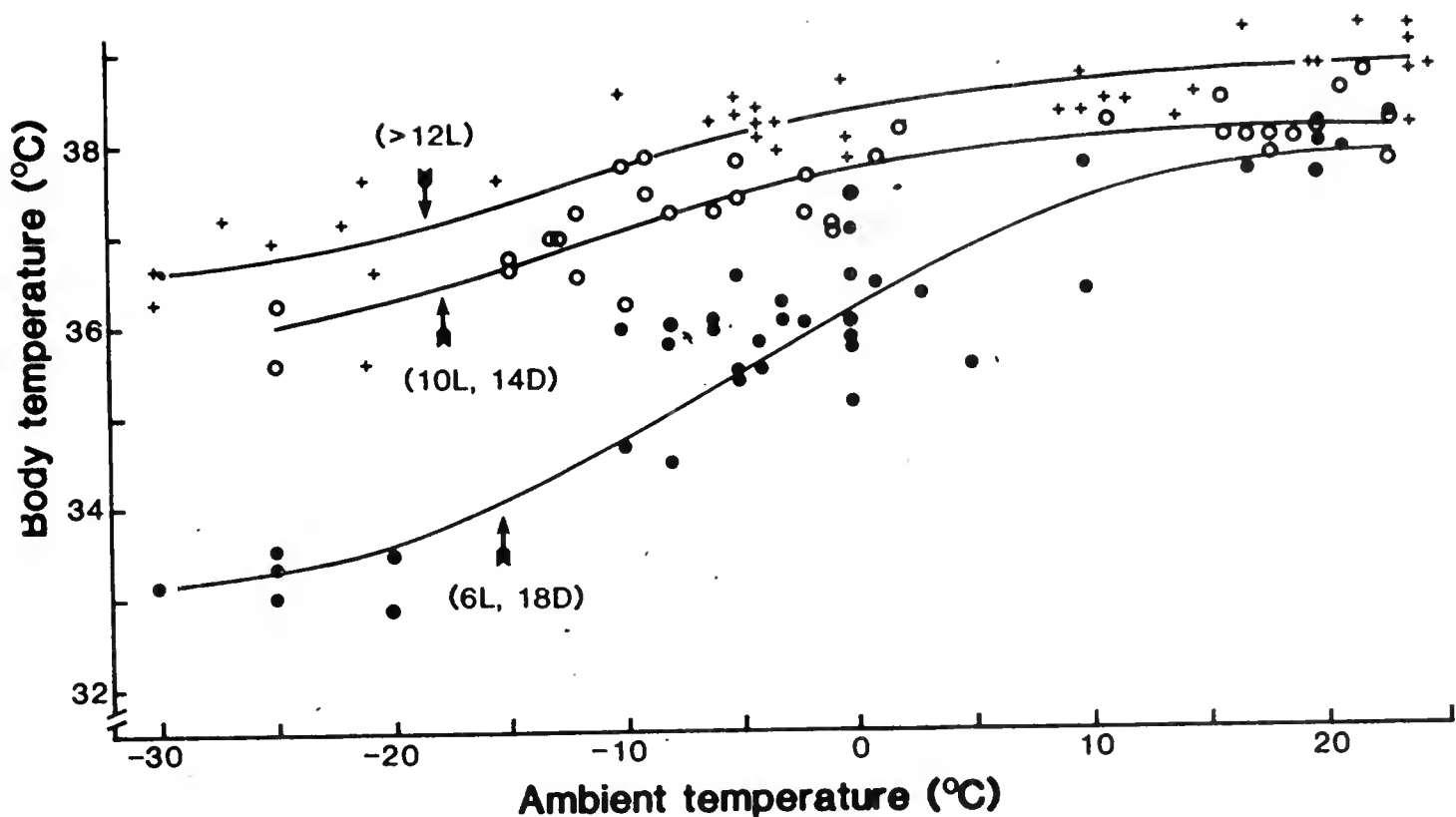


Fig. 15. The relationship between body temperature during sleep and the ambient temperature, for Willow Tits during different seasons of the year and consequently different night lengths. Each point represents the minimum value recorded on each single night. The birds in question were tested in midwinter (6L, 18D; filled circles), in late autumn or early spring (10L, 14D; open circles) and summer ($> 12L$; crosses). The curves are fitted by hand. After Reinertsen and Haftorn

when at rest, the body temperature at roosting time gradually fell until it levelled off at some time between 2100 and 2200 hours. Body temperature thereafter remained more or less constant until two to three hours before sunrise, when it gradually rose to the normal daytime level.

However, the degree of hypothermia exhibited by the tits was dependent on the ambient temperature. The lower the ambient temperature, the lower was the body temperature (Fig. 14). A similar relationship has also been found for the Siberian Tit (Haftorn, 1972), the Black-capped Chickadee (Chaplin, 1976), as well as for Hummingbirds (Wolf, Hainsworth, 1972) and Sunbirds (Cheke, 1971). The results obtained for the Willow Tit indicate that the hypothermic response levels off at ambient temperatures below -20°C and above 20°C (Fig. 15). Furthermore, the Willow Tits showed a marked seasonal variation with regard to the depth of hypothermia achieved when they were exposed to different ambient temperatures. The maximum response was observed in midwinter-acclimatized birds, whereas, on the other hand, mid-summer-acclimatized birds showed almost no response. Between these two extremes a steady gradient was found. This pattern of seasonal relationship is possibly regulated by the photoperiod.

The degree of nocturnal hypothermia observed was apparently a controlled physiological response to the combined influence of low ambient temperatures and long winter nights. I would like to emphasize that all the birds in the experiments conducted re-attained their normal daytime body temperature in the morning, indicating that they were in good physiological condition after the experiments..

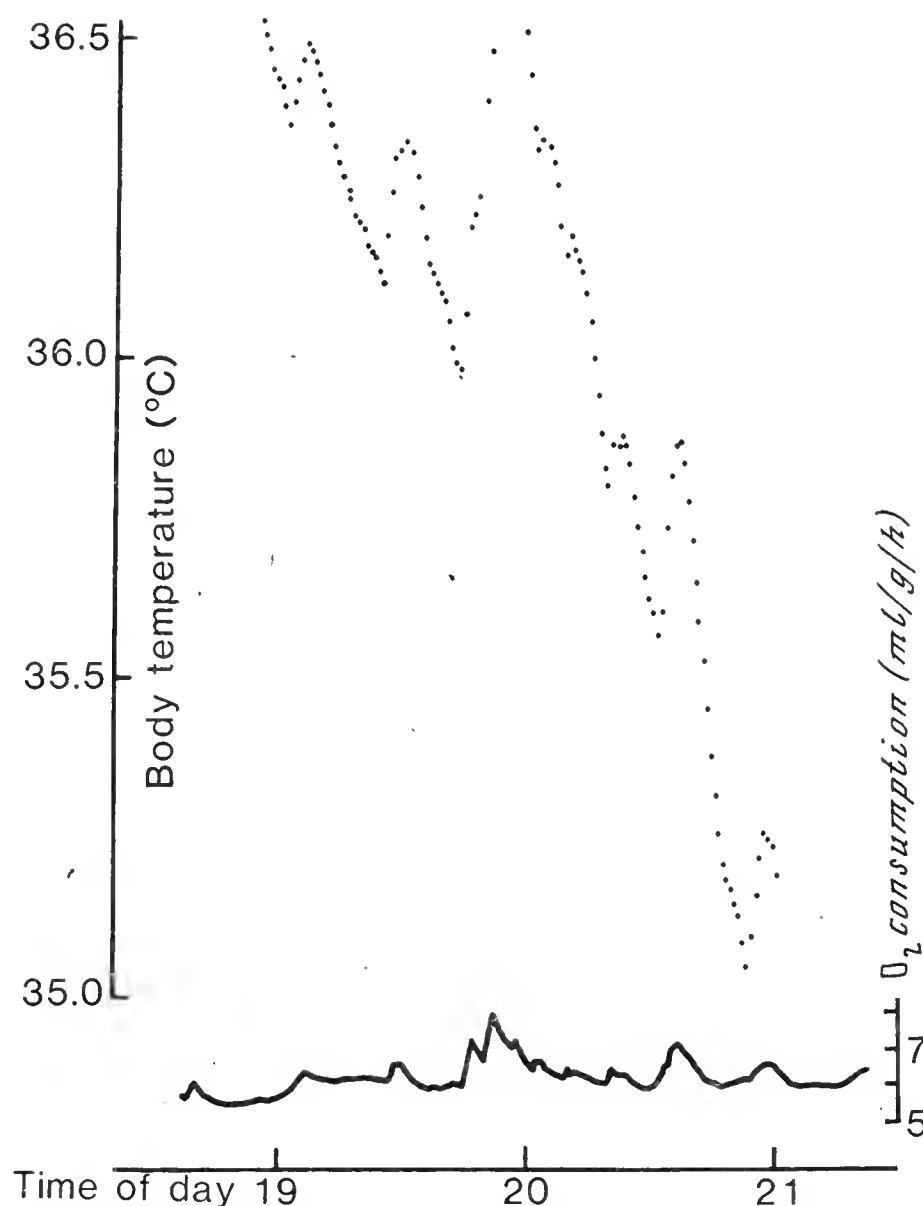


Fig. 16.

Changes in oxygen consumption and body temperature of a winter-acclimatized Willow Tit when entering into sleep at a stable ambient temperature of -10°C . After Reinertsen and Haftorn

The diurnal rhythm of the body temperature of the Willow Tit followed the changes in the length of the photoperiod in the same manner as that previously shown for other species of birds. This indicates that an endogenous rhythm exists, triggered by the photoperiod as a Zeitgeber. The precisely regulated

rate of the rises and falls in body temperature shown in Fig. 16 supports the general theory that body temperature is regulated in relation to a reference value which gradually changes throughout the 24-hour period (cfr. Heller et al., 1978; Haftorn, Reinertsen, 1982).

When the Willow Tits which we studied were exposed to a stable ambient air temperature, the initial decline in body temperature at roosting time coincided with a decrease in the rate of energy expenditure, as measured in terms of oxygen consumption (Fig. 17). It is noteworthy, however, that whereas energy metabolism became stable within an hour, body cooling continued for a much longer time. When body temperature finally became stable, the rate of metabolic heat production corresponded to the heat loss in terms of the following equation $Q = C(T_b - T_a)$.

From this equation it follows that the level of hypothermia has already been predetermined when the rate of metabolism begins to decrease at roosting time, because at a constant ambient temperature, a constant rate of metabolism, and constant conductance, there can only be one specific body temperature at which the bird is in a thermal balance (Reinertsen, Haftorn, in press).

The physiological advantage gained by lowering their body temperature during the long-lasting nightly sleep in midwinter is of course a saving in energy expenditure. However, a low body temperature also means a lower state of alertness and presumably a greater risk of being caught by predators. Hence, natural selection may favour the ability of maintaining as high a rate of metabolism as the bird can afford in relation to its available energy reserves. In other words, the main aim from the bird's point of view is not necessarily to save as much energy as possible. Instead, the energy used could be a trade-off between keeping the state of alertness as high as possible and at the

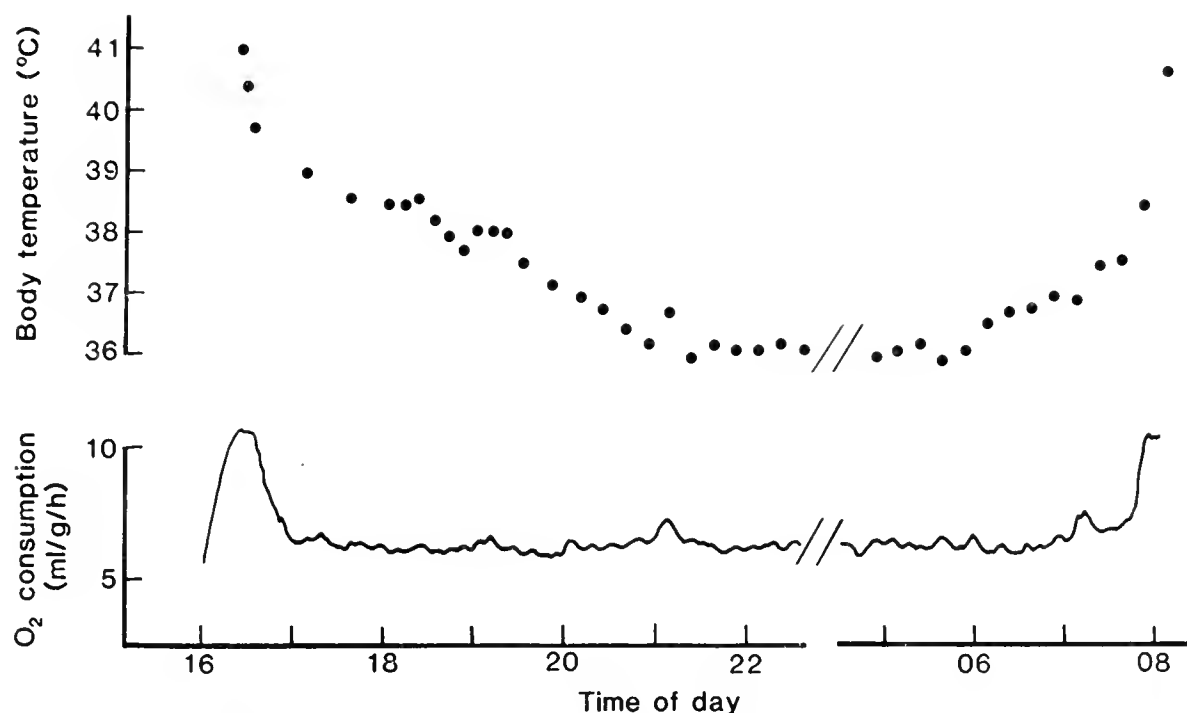


Fig. 17. The oxygen consumption and body temperature of a winter-acclimatized Willow Tit while entering into, during, and emerging from sleep at a stable ambient temperature of 0°C

same time saving sufficient energy to survive the night, including re-emerging from the state of hypothermia in the morning.

From the available evidences we suggest that in the evening, in other words at roosting time, the Willow Tit regulates its metabolic rate at the specific level which corresponds fairly closely to the maximum affordable energy expenditure. And this evening metabolic rate is determined according to at least the following three factors, namely the particular ambient temperature the bird is exposed to, the expected length of the night, and the immediate state of the bird's energy reserves.

One prediction from this hypothesis is that - other factors being equal - a bird which possesses only a low energy reserve would be expected to exhibit a stronger degree of hypothermia compared to a bird with greater energy reserves. The experimental evidence so far does in fact verify this statement, as shown by Figs. 18,20.

Another prediction is that the state of hypothermia during the night will be subject to moderation according to eventual changes in the ambient air temperature. This prediction, too, was verified by our experiments. Thus, when the ambient temperature was lowered, after a bird had once achieved a stable hypothermic level in accordance with the initial temperature to which it was exposed, it immediately responded by further decreasing its body temperature down to a new stable level (Fig. 19). And, conversely, if during the night a bird was subjected to an increase in the ambient air temperature, it immediately responded by raising its body temperature (Fig. 19).

Among the holarctic tits hypothermia has so far been only indisputably recorded for three species, namely the Willow Tit, the Siberian Tit, and the Black-capped Chickadee. Hypothermia has also been reported for the larger-sized species, the Great Tit (Steen, 1958), but the results of recent experiments are not confirmative (Reinertsen, Haftorn, unpublished).

Although no information for other species of titmice is yet available, we may nevertheless draw the tentative conclusion that hypothermia is essential for the night-time survival of small birds wintering in the far north. By

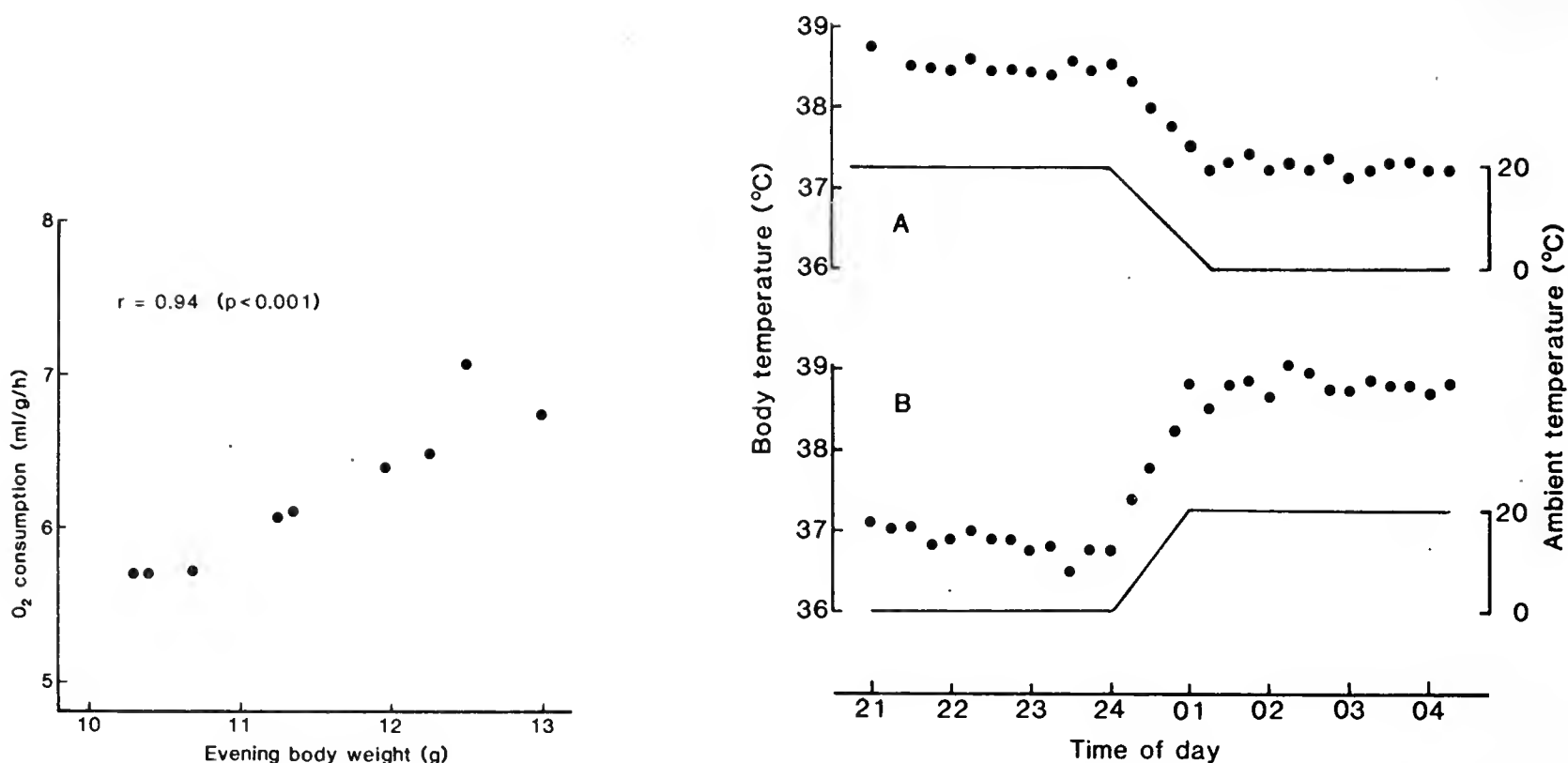


Fig. 18. The relationship between evening body weight and oxygen consumption during the following night (deep sleep phase) for a winter-acclimatized Willow Tit. The ambient temperature during the nights ($n = 9$) was constantly 0°C . After Reinertsen and Haftorn (in prep.)

Fig. 19. Change in body temperature during nightly sleep of a winter-acclimatized Willow Tit as a response of change in ambient temperature. After Reinertsen and Haftorn (in prep.)

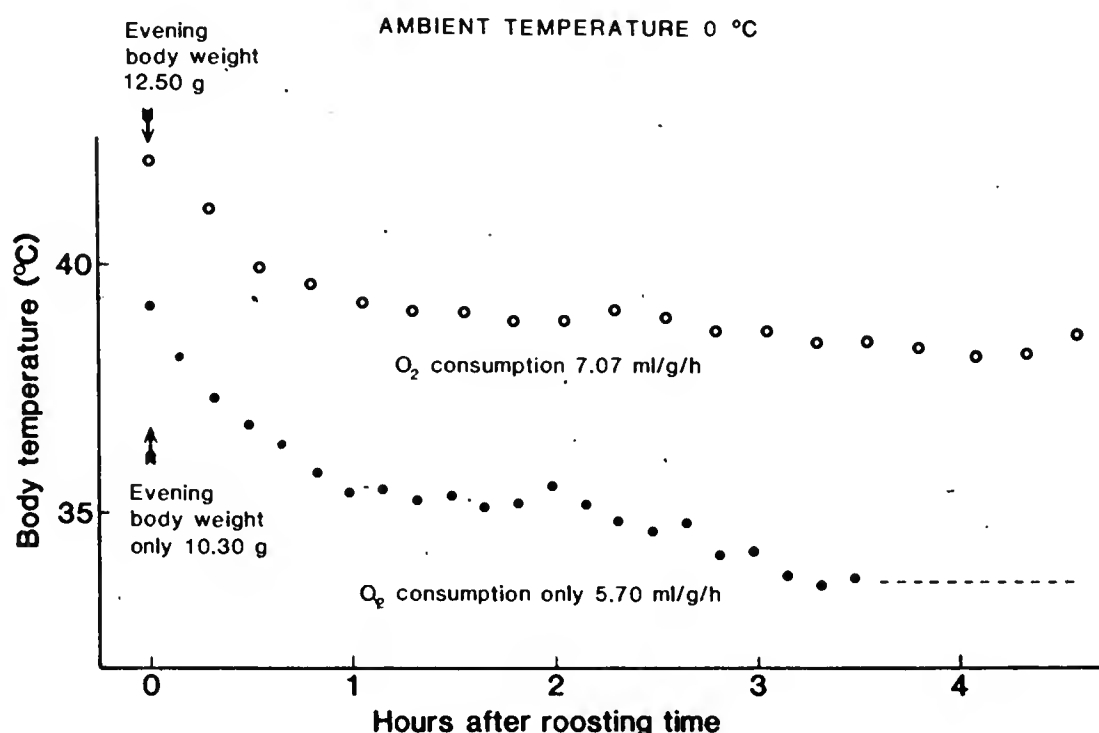


Fig. 20. Body temperatures of a winter-acclimatized Willow Tit (the same individual as composing Fig. 18) during two separate nights before which the bird differed considerably in weight. The ambient temperature was constantly 0°C during both nights. After Reinertsen and Haftorn (in prep.)

lowering their metabolic rate, the titmice can reduce their nightly energy loss by at least 10%, an amount which may easily represent the margin between life and death for such small birds living under the combined stresses of hunger, cold, and long nights.

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SEXUAL IMPRINTING IN ZEBRA FINCHES - MECHANISMS AND BIOLOGICAL SIGNIFICANCE

Klaus Immelmann

Fakultät für Biologie, Universität Bielefeld, Bielefeld, FRG

INTRODUCTION

Imprinting is known and can be defined as an early and fairly rapid learning process with a particularly stable result. The best-known examples are filial imprinting, by which the hatchlings of precocial birds learn the characteristics of their mother or their parents, and sexual imprinting. Sexual imprinting is a learning process during which the young of both precocial and altricial birds learn the species-specific characteristics which, enable them, in adult life, to find a conspecific mate (Bateson, 1966; Fabricius, 1951;) Hess, 1973; Immelmann, 1972b).

Imprinting, for reasons which will be explained in the final discussion has always been a favorite subject in ornithological research and a favourite topic during ornithological congresses.

EVIDENCE FOR SEXUAL IMPRINTING

The present paper does not attempt to present another review of the vast literature on imprinting which has accumulated over the years. It will rather try to present one particular example of imprinting and to address both its proximate side, i.e. to demonstrate the mechanisms which can be involved in its regulation, and its ultimate significance, i.e. to discuss some aspects of the biological function of early learning. The example chosen is the occurrence of sexual imprinting in the Australian Zebra Finch (Taeniopygia guttata castanotis) which has been studied in our laboratory for many years.

In a pilot study, we attempted to determine if and how early social experience has an influence on the choice of a mate. This was done in cross-fostering experiments with another species of estrildid finches, the Bengalese Finch (Lonchura striata f. domestica): male Zebra Finches were foster-reared with Bengalese Finches until they had reached nutritional independence. They were then separated from the foster parents and kept in individual cages.

As soon as they were sexually mature, they were tested in a double-choice situation with a female of their own species and a female of their foster parents' species. All males treated in this way proved to have a clear preference for the foster parents' species (Immelmann, 1969).

Another pilot study was concerned with female imprintability, because in the literature, there has been considerable discussion as to whether in females, as in males, early experience may influence subsequent sexual preferences. Schutz (1965) published a theory based on his experiments with ducks according to which both sexes are imprintable in monomorphic species, whereas in sexually dimorphic species innate recognition of the nuptial plumage of the male plays the most important role for the female. These assumptions have been modified by Klint (1975), who found that female mallards do modify their sexual preferences according to early experience, although they also seem to show a genetically determined preference for the nuptial colouration of the male.

Bossema and Kruijt (1982) have pointed to the fact that directed activity of males used as choice objects is an important factor and that a reason for the differences between the results obtained by Schutz and Klint may be found in this area.

Using a slightly different test situation, a multiple choice apparatus, Sonnemann and Sjölander (1977) tested the preferences of Zebra Finch females raised by Bengalese Finches and of controls raised by their own species. They found a preference for the males of the foster species in the first group and a preference for conspecific males in the control females. They have thus given the first experimental proof of female imprintability in a sexually dimorphic species of birds.

PERMANENCE OF EARLY PREFERENCE

The next approach was towards the two criteria which usually have been thought as being the principle distinguishing characteristics of imprinting: the great stability of its results (frequently referred to as irreversibility) and its restriction in time, i.e. the existence of a sensitive phase during which imprinting takes place (for review, see Immelmann, 1972b).

The possible occurrence of irreversibility was tested in the following way: the foster-reared Zebra Finch males were deprived of any further social contact with members of the foster parents' species but were provided with a conspecific female and with nesting facilities. Most of these males eventually mated with the female and jointly raised one or several broods. After six months, they were separated from their conspecific mate and were tested again in a double choice situation. The results of these tests revealed the same preference for the Bengalese Finch females as was observed before the period of intraspecific contact (Immelmann, 1972a).

This means that the brief contact with the foster parents early in life exerted a longer-lasting influence than did social contact of long-term duration during adult life. It can be concluded that in adult Zebra Finches sexual imprinting is characterized by a degree of stability that justifies the term "irreversible". Similar but not quite as definite stability of sexual preferences acquired early in life has recently been found to occur also in female Zebra Finches (Sonnemann, Immelmann, in prep.)

An interesting detail has to be added here, however, which might throw some light on the character of such durability: During the first test or tests after the end of the intraspecific breeding experience, some of the Zebra Finch males (about 20%) preferred to court the Zebra Finch female and paid less attention to or ignored the Bengalese Finch female. However, subsequent tests revealed that such preferences gradually decreased and finally disappeared, whereas the original preference for the foster species reappeared and increased again. After a number of days, the Bengalese Finch females were courted preferentially or exclusively, just as they had been before the Zebra Finch male's period of intraspecific contact (Immelmann, 1979, see Fig. 1).

It follows that even in individuals with "irreversible" preferences, a new preference can be established in adult life. The point is, however, that the "new" preference will be lost in the absence of continual exposure or reinfor-

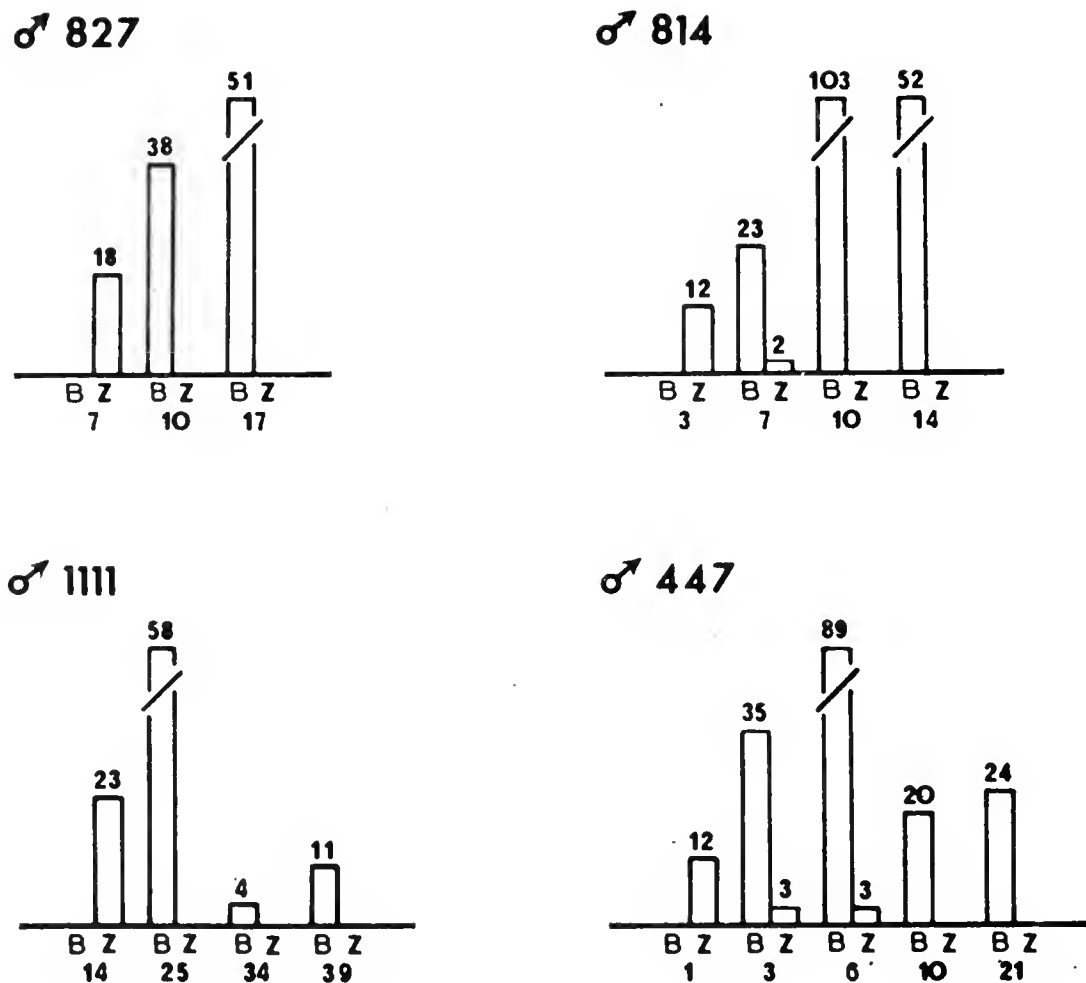


Fig. 1. Transient preference for Zebra Finch females displayed by Bengalese-imprinted Zebra Finch males following intraspecific breeding contact. The numbers on top of the blocks represent the number of courtship sequences directed toward the Bengalese Finch female (B) or the Zebra Finch female (Z) respectively. The numbers below the line give the date of the double-choice experiments (in days after separation from the conspecific female): during the first tests, the males courted only the Zebra Finch female (although a strange female and not the male's previous mate was offered) but returned to the primary preference for Bengalese Finches after a number of days (from Immelmann, 1979)

cement, whereas the original preference established during the sensitive phase is retained indefinitely even without any further reinforcement.

It can be assumed from these experiments that even in a typical case of irreversibility no complete buffering against subsequent acquisition of new social signals is always observed. Instead, for some adult males it has been found that a primary preference can be super-imposed by a secondary one. This does not mean, however, that the first one has been lost. On the contrary, after disappearance of the social object that caused the change in preference, the old preference comes back again. Similar results have been obtained by Cherfas, Scott (1981) for filial imprinting in chicks.

SENSITIVE PHASE FOR SEXUAL IMPRINTING

The next study was concerned with the possible occurrence of a sensitive phase for sexual imprinting, especially with its termination.

Using 337 individuals, this study investigated whether the same degree of irreversibility observed in adult birds can also be demonstrated in adoles-

cents. Male Zebra Finches were again foster-raised by Bengalese Finches, but instead of being kept isolated after separation from the foster parents, they were immediately given intraspecific experience by being placed into a cage with several Zebra Finch males and females. Four series of experiments were run with three, seven, thirty and sixty days of intraspecific contact, respectively. The age at which the birds were transferred from Bengalese foster parents to Zebra Finches varied from day 27 to day 73.

The results can be summarized as follows: for adolescent males, in contrast to adults, it is still possible to alter a previously established preference and to "re-imprint" the birds on their own species. The success of such attempts, however, depends mainly on two variables, the age of the bird and the duration of social contact with its own species. If only three or seven days of intraspecific contact are permitted, such contact must begin no later than around the 40th day of life in order to have any permanent effect on subsequent sexual preferences. On the other hand, if 30 or 60 days of contact are provided, changes of preference are still possible when the bird is placed together with conspecifics at a later age (57 or 71 days respectively).

It follows that the older the adolescent bird is, the more social contact is necessary to change a previously established social preference. In other words, with increasing age the social effort, i.e., the duration of social contact necessary to establish new preferences increases, and this process, as the comparison of the four series indicates, is a gradual one. Obviously, sensitivity to those social stimuli responsible for establishing permanent social preferences decreases by degrees and comes to its definite and gradually rather than abruptly (see Figs. 2 and 3).

Altogether, the sensitive phase study seems to permit two conclusions:

1. The sensitive phase for sexual imprinting in Zebra Finches comes to its close very early in life: Even in the earliest isolates, before day 30, many individuals proved to be imprinted on Bengalese Finches so strongly that no subsequent change through intraspecific contact could be achieved any more. Between about day 30 and 40, some but comparatively fewer changes still occurred, whereas beyond that age the number of changes decreased rapidly.

2. The results revealed a large amount of individual variation: Some individuals seemed to be "closed" very early, and even an extended period of intraspecific contact (30 or 60 days) did not result in a change of their Bengalese Finch preferences any more. Others seemed to "remain open" for a longer period of time and even brief intraspecific contact (three or seven days) led to a change in preferences.

FACTORS INFLUENCING THE ESTABLISHMENT OF EARLY PREFERENCES

Possible functions of such differences have been discussed elsewhere (Immelmann, 1979). However, it also seems to be possible that the variation is, at least in part, the result of variables involved in the experiments. Although it was tried to keep the breeding and testing conditions as constant as possible, there are a few factors for which, mostly for technical reasons, a certain degree of variation could not be prevented. In a multiple-regression-analysis therefore, we attempted to find out which of the variables do have an influence on subsequent preferences for one species or the other.

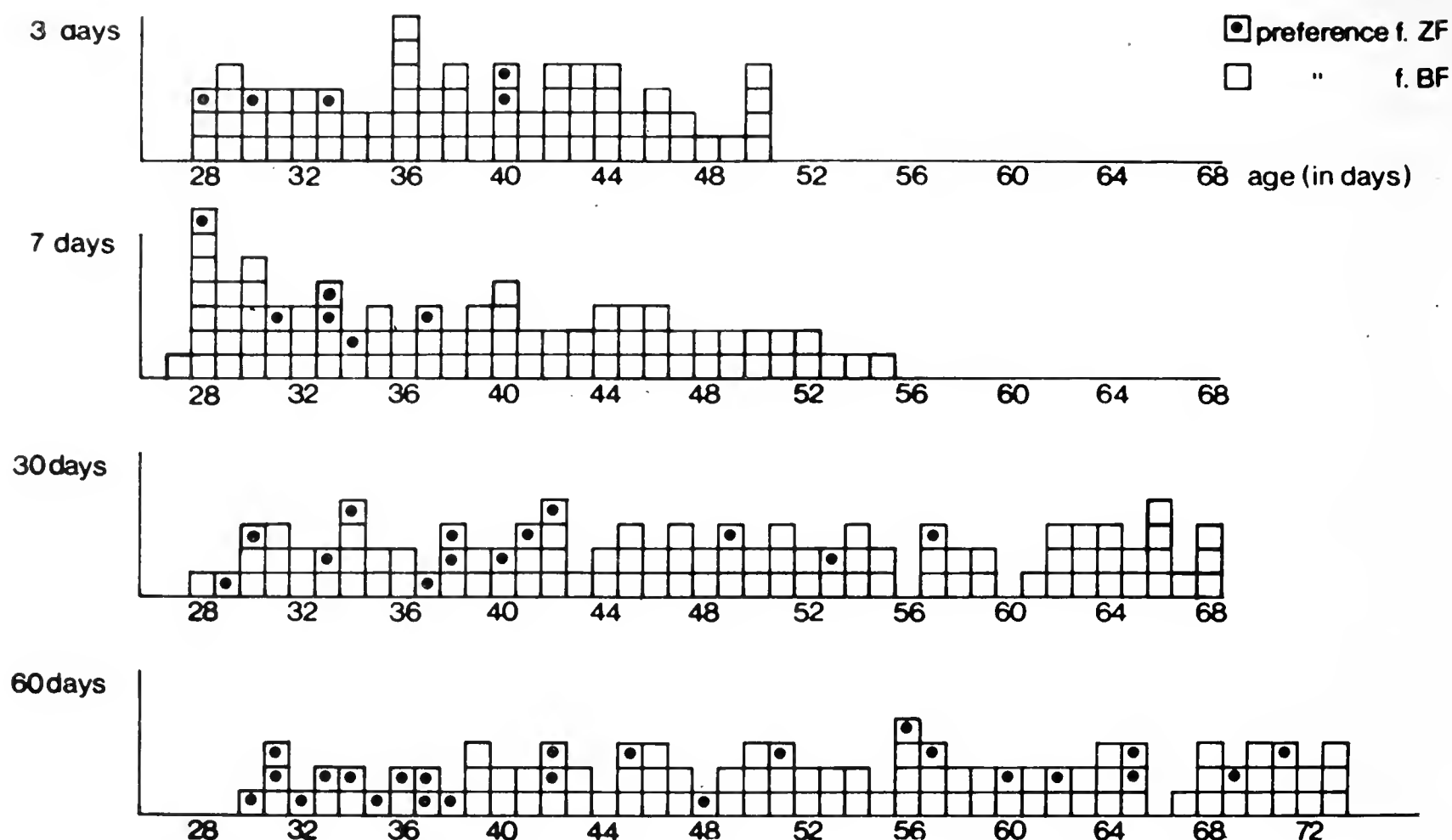


Fig. 2. Sexual preferences of male Zebra Finches reared by Bengalese Finch foster parents and subsequently exposed to conspecific females for 3, 7, 30 or 60 days respectively. The abscissa gives the age (in days) of transfer from the foster parents to the conspecific females. Empty squares represent individuals which, during the choice tests, showed a preference for Bengalese females. Their sensitive phase, therefore, must have come to its close before the day of transfer. The males, represented by squares with a central black dot, in contrast did show a preference for Zebra Finch females. Assuming that at the day of transfer they also had a preference for Bengalese Finches (an assumption seemingly justifiable on the basis of the results of the pilot study) then they must have replaced their primary preference for Bengalese by a secondary preference for Zebra Finches as a result of social contact with the latter (from Immelmann, Suomi, 1981)

The study revealed that except for the two factors already mentioned, the age of the bird and the duration of subsequent social contact with conspecifics, the following variables were found to exert an influence: number of other males in the Zebra Finch group; number of females in Zebra Finch group; number of male siblings; number of female siblings; temporal interval between final isolation and first double-choice test; daylength on the 15th day of month of hatching.

Details of the strength and direction of such influences are explained in Fig. 4. In summary, the results of the multivariate analysis show that with the exception of the interval between final isolation and double-choice tests and with the marked and highly significant influence of the duration of contact with conspecifics already mentioned, all other variables pushed the preferences towards the foster parents species or, in other words, decreased the probability that a change in preference from Bengalese to Zebra Finch would occur (Immelmann, Goedeking, in prep.).

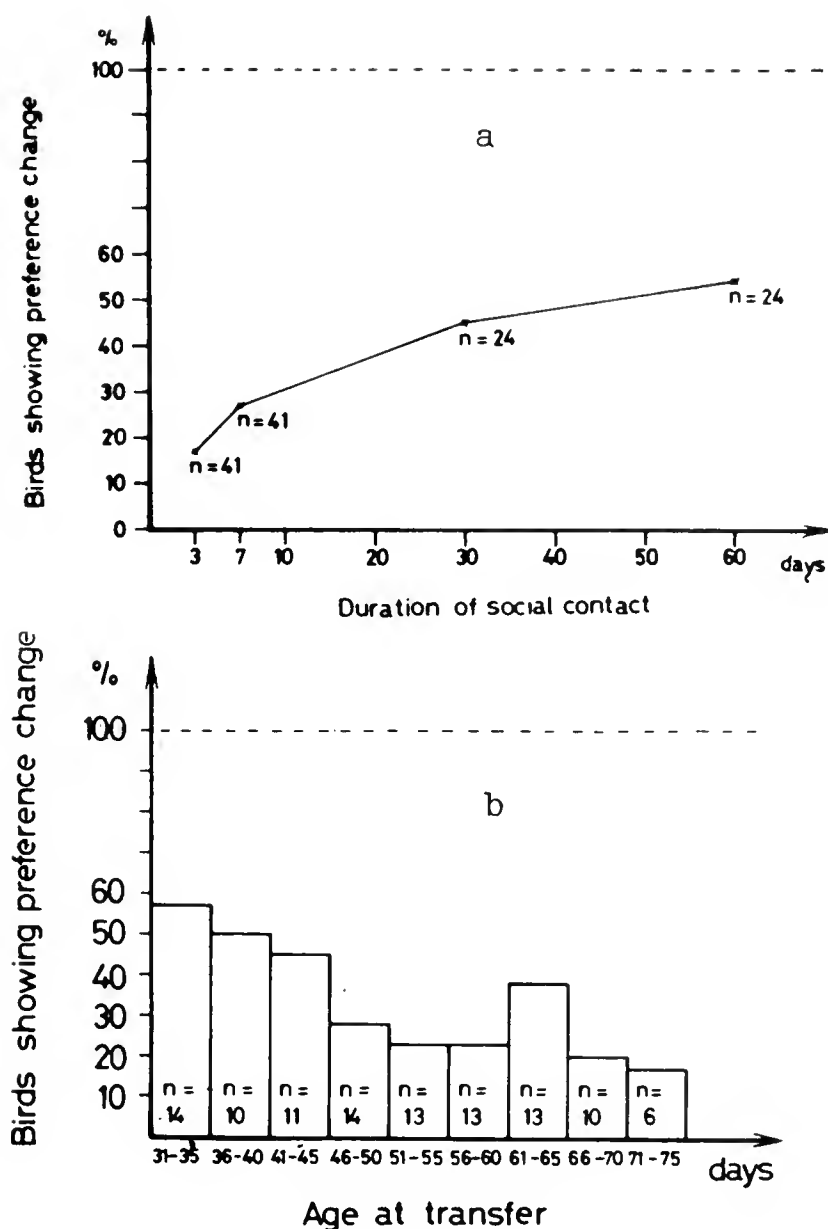


Fig. 3. The data demonstrate the effect of both the age and the duration of social contact for determining the sensitive phase: a - with increasing age (shown here for the 60-day-group) the percentage of changes in preference decreases; b - an extended duration of social contact with Zebra Finch females (shown here for the birds isolated from their foster parents between 28 and 40 days of age) increases the percentage of change in preference

For various reasons, the influence of siblings, especially the direction of such influence, seems to be of special interest. It is surprising that it was possible to prove, in several hundred individuals and with a high degree of significance, that the more male siblings a young Zebra Finch male was raised with the more it will subsequently prefer his foster parents' species, i.e. Bengalese Finches. One would in fact expect such influence to be in the opposite direction, as siblings do offer some contact with the bird's own species which, as shown by the results of the sensitive phase study, may have some influence on subsequent preferences. Kruijt et al. (1983) under slightly different experimental conditions, has indeed evidence that the presence of siblings "can cause at least some sexual interest for Zebra Finch females in many cross-fostered males."

To investigate the influence of siblings further, the males were subdivided into groups according to the age at which they were transferred from their Bengalese foster parents to conspecific females. After the transfer, males had no further contact with siblings. The four subdivisions of age at transfer were: 28-31 days of age, 32-39 days, 40-50 days and 51-73 days of

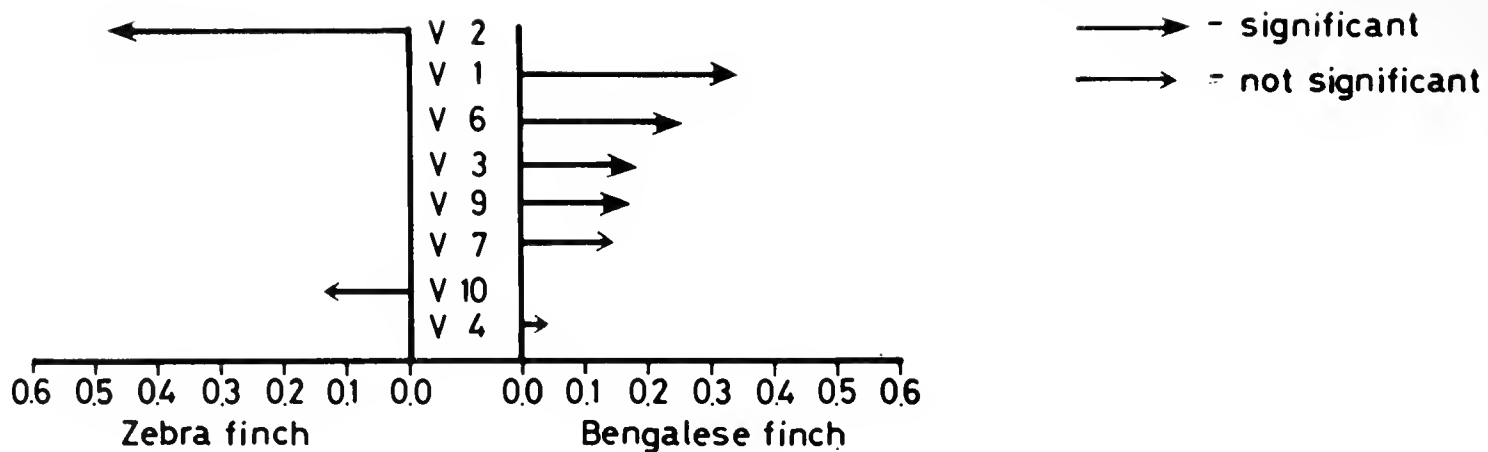


Fig. 4. Direction and strength of variables influencing the establishment of early preferences. An arrow pointing to the right means that this variable influences the young Zebra Finch males to prefer Bengalese Finch females. The intensity of influence is expressed by the "Beta score" of a "standardized regression coefficient", i.e. it is zero if a variable has no influence and is -1 or +1 if a variable has a very strong influence. Significance on the 5-percent-level or better is indicated by bold arrows. An arrow pointing to the left means that this particular variable influences the sexual preference in the direction of the Zebra Finch female. This does not mean that the bird will prefer Zebra Finches absolutely but that it will court Zebra Finches more than it would do without the influence of this particular variable. In other words the variable reduces any absolute preference for Bengalese Finches. (The statistical analysis has been conducted and the figure has been designed by Philipp Goedeking). V 2 - Duration of contact with conspecifics after transfer from foster parents; V 1 - Age at transfer; V 6 - Number of male siblings; V 3 - Number of males in Zebra Finch group; V 9 - Daylength on the 15th of month of hatching; V 7 - Number of female siblings; V 10 - Interval between final isolation and double-choice test; V 4 - Number of females in Zebra Finch group

age (Fig. 5). Such analysis showed that the negative influence of siblings was strongest in the "early isolates", i.e. in the group which was transferred between day 28 and 31; it decreases between days 32 and 39 and becomes stronger again afterwards.

These results indicate that the influence of siblings on subsequent preferences is not a uniform one. It is stronger with regard to siblings than to female siblings. Furthermore, male sibling influence seems to have a certain age-dependency. The way how siblings exert their influence is still open to speculation. Some indications may come from the fact that for the "early isolation group" separation from their (foster) parents was done at a "natural" time, i.e. at the age when in the field, young Zebra Finches leave parents and join the flocks of other juvenile and non-breeding birds which are always present in the vicinity of breeding colonies (Immelmann, 1962).

Field and laboratory observations have shown that at this age, i.e. shortly before and at the time of weaning, there is a considerable amount of aggression between siblings. Perhaps it is such aggression which is responsible for the negative influence brothers exert on each other which in turn leads to an increase in the preference for the (foster) parents.

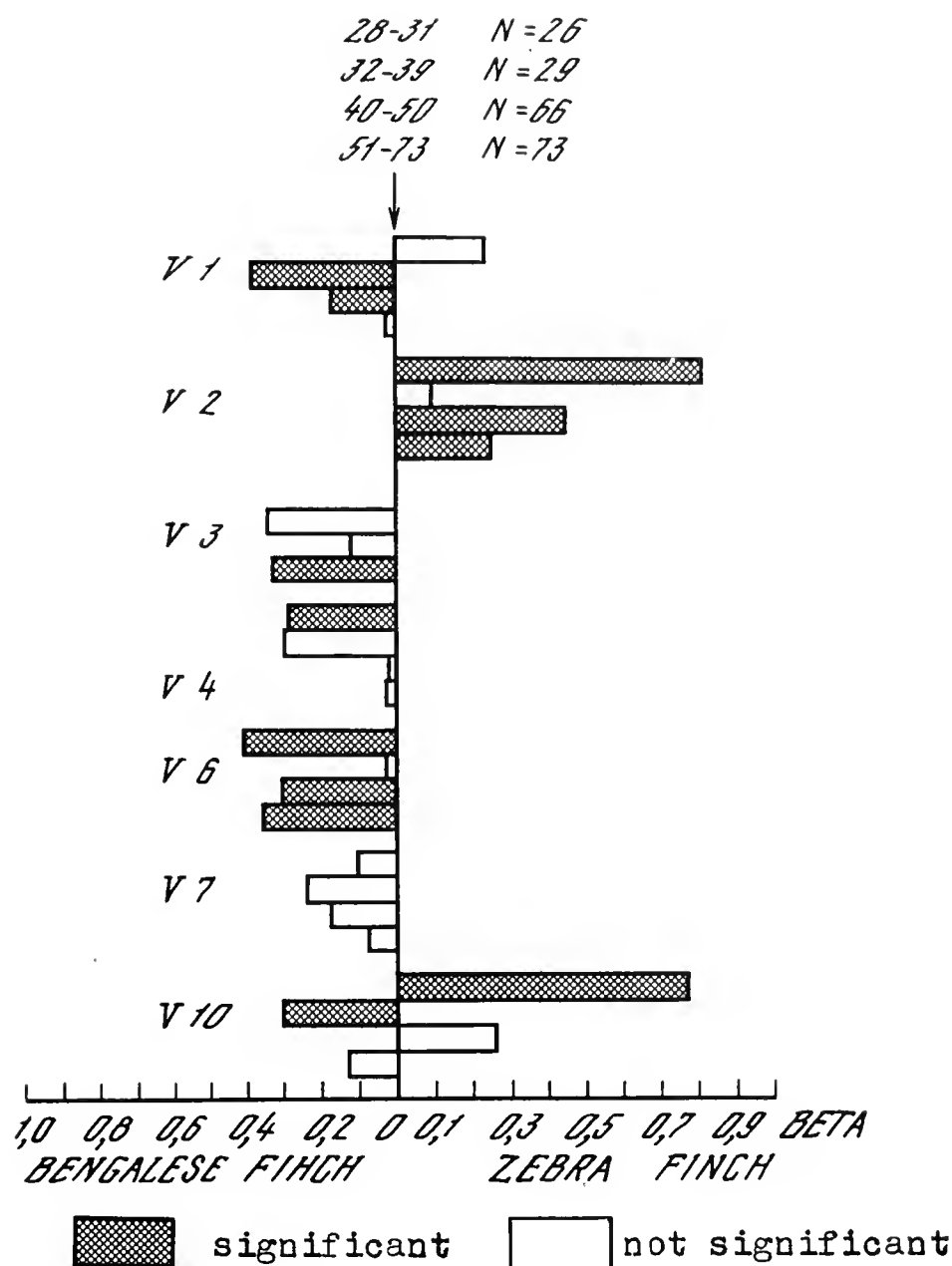


Fig. 5. Age dependency of the variables mentioned in Fig. 4.

After this age, aggression decreases until it increases again as sexual maturation of young Zebra Finch males proceeds. In this latter case, however, it cannot be regarded as specific brother-brother aggression any more but rather as general aggression between adolescent males which frequently occurs in the flocks of non-breeding birds (Immelmann, unpubl. field-observ. 1982). This assumption is supported by the fact that the negative effect of other males in the group of conspecifics also increases with age and for the 51-73 day group is almost identical with the sibling influence (see Fig. 5). These considerations may also help to explain the differences between our findings and those by Kruijt et al., (1983). Kruijt isolated his birds as late as at day 60 when young males have already changed partly into adult plumage. So he did not specifically ask for the influence of siblings during the particular time when brothers are close together under natural conditions.

In the literature on imprinting, quite different statements about the influence of siblings on subsequent mate choice have been made for different species or even for the same species.

In four species of pigeons, Brosset (1971) found that siblings "play no role in the determination of sexual choice". The same was found in colour imprinting of domestic pigeons (Warriner et al., 1963) and by Stamm and Blum for colour imprinting in Budgerigars (*Melopsittacus undulatus*). In the lesser Snow Goose (*Anser caerulescens*) both parental and sibling colour influence mate choice (Cooke et al., 1976). In the Mallard (*Anas platyrhynchos*), Schutz (1965) and Klint (1978) found that siblings do have an influence. They disagree with

regard to the weight of such influence, however, which has been assumed to be smaller than that exerted by the mother by Schutz but of considerably greater importance (about 75%) by Klint.

A possible explanation for the biological significance of the distinctly negative influence of at least male siblings which in our study has been found for the Zebra Finch may perhaps be sought along the following line: young Zebra Finches look different from adults. The biggest difference is in beak colour which is black instead of bright red. If siblings would have a positive effect, therefore, this would imply the danger that young males also develop preferences for specific characteristics of immature birds. The function of negative mutual influence at this age, therefore, may be to avoid the formation of such preferences. In those species, on the other hand, in which mother and siblings look similar, as in the mallard, mother and sibling imprinting "work together in the same direction" (Klint), and a similar danger does not exist. According to Klint (1978) this might be a reason for the great influence of siblings he found in his experiments.

POSSIBLE ROLE OF IMPRINTING IN SEXUAL ISOLATION

Under natural conditions, the preferences acquired through early experience certainly contribute to sexual isolation from other species. For the Australian estrildid finches, precise mechanisms for "species recognition" are essential, as several, sometimes closely related and very similar, species occur sympatrically and even in mixed flocks and breeding colonies (Immelmann, 1961). In captivity, hybrids between these species are common (Immelmann, 1982).

A next step in our investigations, therefore, was concerned with the question of whether early experience does indeed exert an influence on the permanent choice of a mate and if it will do so under more natural conditions than in the double- and multiple-choice cage-situations used so far.

In order to study the role of early experience on sexual isolation, an intraspecific cross-fostering experiment with Zebra Finches was conducted using "wild-coloured" (naturally grey) individuals and members of a leucistic morph which are white in plumage colour. A total of 64 birds (32 ♂ 32 ♀) of both colour morphs were used. Half of the birds were raised by their own parents, the other half by foster parents of the other colour morph.

The birds were separated from their parents or foster parents at an age of 40(±1) days. They were then kept in visual isolation until they had reached sexual maturity when they were introduced simultaneously into a large flight cage 22 x 8 x 5 m, which was planted with small trees and furnished with nest boxes. The behaviour of the birds, the use of roosting nests and the occurrence of pair-formation was recorded. Within three days 61 of the 64 birds, irrespective of their own plumage colour, had chosen mates which were consistent with their early experience (Fig. 6). Furthermore, with only two exceptions each bird selected partners which were in turn imprinted on its own plumage colour. A wild-coloured male, for example, which was reared by white foster-parents not only courted only white females but in addition he selected as a mate a white female which was foster-reared by wild-coloured birds and so in turn was imprinted on wild-colour. All aspects of the sexual behaviour of the birds and the social structure of the group were in agreement with results obtained during previous field observations in Australia (Immelmann, 1962). During the ex-

Fig. 6. Types of pairs which formed during the sexual isolation experiments: gr/gr symbolizes a grey (wild-coloured) bird raised by grey parents, gr/wh indicates a grey bird raised by white foster parents etc. 61 of the 64 birds selected mates which were consistent with their early experience, one bird was paired with the "wrong" colour morph and two birds remained unmated. (The uneven numbers are a result of the fact that in one pair the ♂ was paired consistent with its early experience while the female was not,) From Immelmann et al. (1978)

| | | mated | | | | |
|-----------|-------|-------|-------|-------|-----------|----|
| ♀ \ ♂ | gr/gr | gr/wh | wh/wh | wh/gr | not mated | Σ |
| gr/gr | 8 | - | - | - | - | 8 |
| gr/wh | - | - | - | 8 | - | 8 |
| wh/wh | - | - | 7 | - | 1 | 8 |
| wh/gr | - | 7 | 1 | - | - | 8 |
| not mated | - | - | - | - | - | 1 |
| Σ | 8 | 8 | 8 | 8 | 1 | 32 |

periment, 31 pairs produced clutches and showed normal incubation behaviour (for details, see Immelmann et al., 1978).

Two conclusions can be drawn: (1) Imprinting on the plumage colour of the (foster) parents may lead to complete sexual isolation between individuals which have different imprinting experience early in life. (2) Such isolation is achieved by both sexes, which again gives evidence that females are as im- printable as are the males.

POSSIBLE ROLE OF IMPRINTING IN SEX RECOGNITION

From previous observations, more or less casual ones, it is known that Zebra Finches obviously do not recognize members of the opposite sex by some kind of an inbuilt mechanism. Zebra Finch males foster-raised by Bengalese Finches, for example, do court Zebra Finches if no Bengalese Finches are present. But in this case, they court females and males and do not seem to make any distinction whatsoever. In order to study the possible influence of early experience on sex discrimination we increased the sexual differences in plumage colour above the natural amount by using mixed pairs of parents with a white male and a wild-coloured female and vice versa. The preferences of males and females raised in this way were tested in a double-choice and a multiple-choice situation respectively. The results revealed a difference between sexes. They showed that males have a clear preference for the plumage colour of their mother whereas females prefer the colour of their father (Immelmann, Sjölander, in prep.). Obviously, sons use their mother and daughters use their father as a model for establishing future mate preferences. Thus, in this dimorphic species there is a constraint on the outcome of sexual imprinting which produces different results in males and females, despite the fact that they are reared together by the same parents (see Table 1).

The mechanisms which might be involved in the sex-specific selection of a model for imprinting are not known yet. One possibility would be that the parents distinguish between male and female offspring and treat them differently. Recent observations by Balda (1982) indicate that there is a sexual di-

T a b l e 1. (a) Preference for wild-coloured females in males raised by a white father and a wild-coloured mother. Out of 42 males, 29 had a more than 90% preference for wild-coloured females, another four males had a more than 80% preference and only one had a preference for white females (I). (b) The opposite situation: Out of 20 males raised by a white mother twelve had a more than 90% preference for white females(I)

II - Number of birds.

| a | | | | b | | | |
|----|---|-----|----|----|---|-----|----|
| I | | II | | I | | II | |
| 0 | - | 9 | - | 0 | - | 9 | - |
| 10 | - | 19 | 1 | 10 | - | 19 | - |
| 20 | - | 29 | - | 20 | - | 29 | 2 |
| 30 | - | 39 | 1 | 30 | - | 39 | 1 |
| 40 | - | 49 | 1 | 40 | - | 49 | 1 |
| 50 | - | 59 | 1 | 50 | - | 59 | 2 |
| 60 | - | 69 | 2 | 60 | - | 69 | - |
| 70 | - | 79 | 3 | 70 | - | 79 | 1 |
| 80 | - | 89 | 4 | 80 | - | 89 | 1 |
| 90 | - | 100 | 29 | 90 | - | 100 | 12 |

morphism in the begging calls of young Zebra Finches which might provide a basis for sex-dependent parent-offspring-relations.

Another possibility is that the young in turn react sex-dependently to such behaviour from the parents and parhaps also from other birds. More specifically there is a tendency in Zebra Finch fathers to show increasing aggression towards the young as independence approaches, and this aggression might well be sex-dependent, either because the sons are recognized as males or because they respond to aggression in a different way than daughters do. The aggression shown by the father may become associated with him and with males in general, and this could then act as a future deterrent for young males to approach other males. In females, on the other hand, similar tendencies could be overcome by the courtship of the male, as has already been suggested by Morris (1954).

ROLE OF EARLY EXPERIENCE ON INDIVIDUAL RECOGNITION

In the research on what is usually called sexual imprinting, i.e. on the early establishment of subsequent mate preferences, a marked shift in interest has occurred recently: whereas in earlier studies "species recognition", i.e.. preferences for species-specific characters, have been of primary interest, some of the more recent work has concentrated on preferences for more subtle characters characterizing, for example,close kin or particular individuals (see for example, Bateson, 1978; Miller, 1981). Some recent studies have shown that in the Zebra Finch, like in other species of birds (Beer,

1970), recognition of particular individuals is also possible and that early experience may again play a role in the establishment of relevant preferences. Using auditory choice tests with songs played from loudspeakers on both sides of a test cage, Miller (1979) found that after a period of two months of separation while attaining sexual maturity, 17 out of 24 Zebra Finch females preferred the song of their own father to the song of another Zebra Finch male. Thus Zebra Finches can recognize their father's song as a consequence of early experience even if followed by a relatively long period of separation. Sjölander, Ronchi (in prep.) have experimental evidence that such preferential reactions to the father are acquired during the short time between leaving the nest (at about 21 days of age, Immelmann, 1962) and about day 40 and that they can be retained for over two years. Such preferences do not necessarily reflect sexual preferences though and, therefore, do not give evidence for sexual imprinting. They demonstrate, however, that in the Zebra Finch, early experience does not only exert a crucial influence on the establishment of preferences for species-specific characteristics which might help to prevent hybridization with other species. Rather such early experience also helps to establish preferences for the opposite sex or for individual characters which might also contribute to kin recognition.

MECHANISMS

After having collected numerous data about the different aspects of the influence of early experience on mate choice it is tempting to look for possible physiological mechanisms which might be involved in imprinting, especially in the regulation of sensitive phases and in the stable maintenance of early preferences. One mechanism could be hormonally based (for review see Landsberg, 1981). In the male Zebra Finch, as in other vertebrates, male courtship behaviour is dependent on male sexual hormones. Such correlation has been demonstrated by castration experiments and subsequent hormone substitution, by "chemical castration" by means of antiandrogens, and by determining the androgen levels of the birds by radioimmunoassay. In the latter experiment, Pröve was able to find a positive linear correlation between the amount of courtship behaviour in standardized courtship tests and the amount of testosterone in the blood plasma (for details see Pröve, 1974, 1978; Arnold, 1975; Pröve, Immelmann, 1982).

In order to elucidate whether androgens are also involved in the regulation of sensitive phases for the establishment of sexual preferences, a longitudinal study on the development of androgen levels in male Zebra Finches was conducted. From 28 individuals blood samples were taken every four days starting at an age of only eight days until about 75 days post hatching (Fig. 7). Analysis of the samples revealed that testosterone levels in adolescent male Zebra Finches do not increase gradually. Instead age periods characterized by very active steroid biosynthesis alternate with stages of relative inactivity. The peaks occur at an age of 18-22 and at 34-38 days. At the age of about 70 days, adult levels are finally reached (Pröve, 1983).

If one looks at the natural history of the Zebra Finch, two temporal correlations become apparent: The first peak in testosterone level coincides

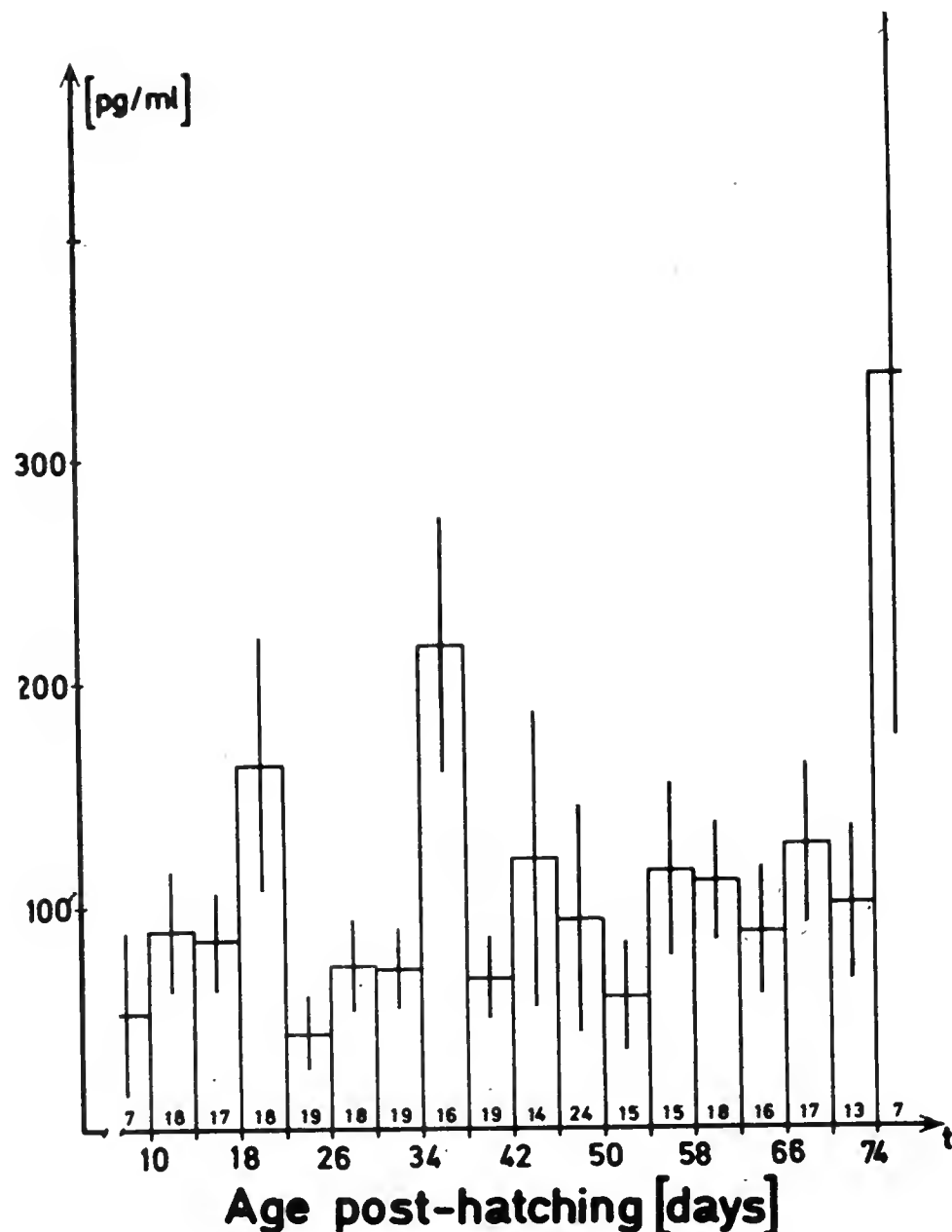


Fig. 7. Testosterone development in male Zebra Finches. Starting at day eight post-hatching the means of the hormone measurements from individual male Zebra Finches were calculated at four day intervals. Columns - means; vertical lines - \pm S.E.M.; numbers under each column are the sample size for each mean (from Pröve, 1983)

with the age at which the young leave the dome-shaped nest and, for the first time, see their parents in full size and colour (Immelmann, 1962). Although no immediate data are available yet, it seems to be possible that during this period of time the offspring are particularly sensitive to social stimuli from the parents. This assumption is in accordance with the results presented earlier indicating that most individuals proved to have stable preferences as early as before 27-30 days of life (see Fig. 2).

The second peak at the age of 34-38 days occurs shortly after weaning, i.e. after the young Zebra Finches leave their parents to join the flocks of non-breeding birds.

Such temporal parallels between periods of increased testosterone level and periods of presumably high sensitivity to social stimuli might be seen as indications that there is also a causal relationship. In a second step, therefore, an attempt has been made to influence the imprinting process itself by administration of different steroids during the sensitive phase, starting at an age of ten days up to day 35 post hatching. The results available so far indicate that in the testosterone-treated males, imprinting on the species of the foster parents seems to be even stronger than after "normal" cross-fostering: no sexual behaviour towards Zebra Finch females was observed in any of the androgen-treated birds during the double-choice experiments (Pröve, 1983).

No conclusions can be drawn yet about the way testosterone may influence sensitivity to imprinting stimuli. It may lead to a general increase in the rate of brain metabolism or to an increase only in particular brain areas.

Testosterone may have organizational effects on certain areas of the CNS as has been found in other species (for review see MacLusky, Naftolin, 1981). On the other hand, its influence may only be an indirect one, e.g. an increase of aggression between siblings or the facilitation of initial sexual motivation.

Another regulatory mechanism that could be involved in the timing of sensitive phase is the central nervous system. It seems to be possible that phase specificity in the establishment of social and other preferences is paralleled by a similar specificity in the development of certain brain areas, those areas that are involved in the regulation of the relevant behaviour systems and in processing the necessary sensory stimuli.

Research along this line has to involve two steps: First, one has to find which areas of the brain, in the Zebra Finch, are involved in the processing of imprinting stimuli, and second one has to see if these particular areas do indeed exhibit some phase specificity in development.

Knowing that sexual imprinting in Zebra Finches mainly involves visual signals, a study of visual centers in the CNS was conducted. By injection of Horse Raddish-Peroxydase (HRP), Nixdorf and Bishof (1982) have traced distinct visual pathways from the retina to two regions of the telencephalon, the visual wulst and the ectostriatum. It is not known yet which of these two pathways can be related to the processing of stimuli relevant for imprinting. However, histological studies by Wolff and Teuchert have shown that in the ontogenetic development of the so-called tectofugal pathway leading to the ectostriatum, a distinct phase-specificity occurs: This specificity refers to the phenomenon of physiological cell death, i.e. the elimination of early neurons that had already had functional contacts. Such early neurons are replaced by other neuronal systems which need sensory input for appropriate synaptogenesis. In the Zebra Finch, there is a close coincidence between the time course of such axonal degeneration and the time of maximum sensitivity for sexual imprinting, with the degeneration occurring immediately before the onset of the sensitive phase for sexual imprinting, which has been found to occur shortly before the 15th-20th day of age (Immelmann, 1972a). Such correlation is obvious in the tectum opticum and in the nucleus rotundus (Wolff et al., in prep.).

Based on their neuroanatomical studies Wolff and Teuchert propose that such physiological degeneration of synapses and/or synaptically connected neurons might induce a specific localized and transient potential for reactive synaptogenesis. It seems to be possible that the establishment of long-lasting preferences is achieved through the selective formation of new and particularly stable axonal and dendritic connections (for further discussion, see Bischof, 1979, 1984).

DISCUSSION

In this paper, I have tried to demonstrate the way in which early experience in one particular species of bird, the Zebra Finch, may influence the choice of a mate, and to create as complete a picture as possible of the factors involved. In concluding it seems to be appropriate to discuss the possible biological functions of such sexual imprinting by asking two questions:

What are the specific advantages of imprinting-like learning, and why is this type of learning particularly wide-spread in birds?

The function of imprinting-like learning may be found in a combination of the relevant advantages of "closed" and "open" programs in the sense of Mayr (1974). Closed programs which are characterized by a high degree of - probably genetically determined - predetermination warrant for the necessary information being available as soon as it is needed during the individual life cycle. Open programs, on the **other hand**, are characterized by a higher degree of accuracy because in general, the amount of information that can be stored in the genome tends to be smaller than the possible amount of information **which can be stored in the memory**. Consequently, object preferences based on learning tend to **include** more details and will thus be more precise than those based on genetic factors (for discussion, see Mayr, 1970, Immelmann, 1975).

Imprinting combines these functions. Due to the early and rather brief sensitive phases and the subsequent stability of imprinted preferences it guarantees that relevant information is being gathered quickly, and that such information is available at or - in the case of sexual imprinting and perhaps some other imprinting-like processes - even before it is needed for the first time. In addition, the temporal restrictions typical for imprinting processes ensure that there is a maximum of sensitivity just at the time when conditions for learning are also at their optimum. Sensitive phases for, **e.g. sexual**, habitat or locality imprinting, have been found to coincide closely with the time when the young animal is surrounded by family members and living in an environment which has proved to be suitable for the reproduction of that particular species (for review, see Immelmann, 1972b; **Immelmann**, Suomi, 1981). At a later age, learning of social and non-social characteristics would not only be more difficult but, if the individual, **e.g.** in its winter quarters or during migration, has to live in less suitable habitats and comes into close contact with other species, such learning might even involve the danger of acquiring some "wrong" information. Early availability and a high degree of stability of information, otherwise only provided by "innate" preferences, certainly do confer some selective advantage. In imprinting, they are combined with a degree of early "openness" that allows the individual to adapt to its present social and non-social environment and thereby to any changes in such environment should they occur from one generation to the other.

In addition to these general advantages of imprinting over predetermined preferences as well as over a constantly high degree of openness throughout life, there seems to be a specific advantage of imprinting-like learning with regard to birds: ontogenetic development of birds, as compared to mammals, is characterized by its rapid speed: Birds may reach their adult size and weight within about 1% of their total life expectancy, whereas some mammals need up to 30% (cf. Frazer, 1977; Hendrichs, 1978). Such speed in general development **has been understood as an adaptation to a quick acquisition** of the ideal ratio between body weight and a constant wing surface (Mayr, 1963). It may also be a consequence of a high mortality rate which, at least in **smaller species of birds**, makes several broods per year necessary and leads to an early dispersal of the young. Young birds, as compared to mammals, seem to have "less time" for the acquisition of rele-

vant information and a strong selection pressure towards a rapid development of learning and memory seems to be plausible. These assumptions might provide a possible explanation of why imprinting is more common in birds than it is in mammals. It is **certainly** not by chance that imprinting not only was first discovered but is also most intensively studied in avian species.

SUMMARY

Australian Zebra Finches foster-reared by Bengalese Finches show a social preference for members of the foster parents' species. This statement applies to males as well as to females. The preference is very durable: In adult males no change could be achieved even through several months of reproductive contact with a conspecific female. After such intraspecific contact, however, transient preferences for conspecific females have been observed. Although they only last for days or weeks, but they throw some light on the phenomenon of "irreversibility".

In foster-reared adolescent male Zebra Finches, a permanent change in preference towards Zebra Finch females is still possible. Its likelihood decreases with age, but increases with the duration of intraspecific contact. Siblings do also exert an influence: the more Zebra Finch siblings a Zebra Finch male is raised with, the stronger is the sexual preference it develops for the species of its foster parents.

Intraspecific cross-fostering between white and wild-coloured (grey) Zebra Finches leads, under semi-natural conditions, to a complete sexual isolation between individuals of different plumage colour and different early social experience. In the offspring of mixed pairs of (foster) parents (grey male and white female and vice versa) sexual preferences proved to be sex-dependent: males showed a preference for the colour of their mother, females preferred the colour of their father.

Testosterone treatment during the sensitive phase for sexual imprinting seems to increase the effects of early social experience on subsequent preferences.

The biological significance of sexual imprinting in Zebra Finches is discussed. Imprinting offers a combination of the advantages of genetically determined preferences (availability at the time when the relevant information is first needed) with those of acquired preferences (high degrees of accuracy).

ACKNOWLEDGEMENTS

I want to express my sincere thanks to Ragna Pröve, who did most of the choice experiments reported in this paper, and to Philipp Goedeking, who did the multivariate analysis. I also thank Dr. Colin Barnett, Dr. Hans-Joachim Bischof, Jörg Böhner, Dr. Gunvor Pohl-Apel, Dr. Ekkehard Pröve, and Dr. Roland Sossinka for their lasting assistance and many helpful discussions. I also thank Dr. Jaap Kruijt for his comments on the manuscript. Special thanks are due to Colin Barnett for his help with the English manuscript.

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THE BIRDS OF WESTERN AUSTRALASIA

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THE PROBLEM OF MORPHOLOGICAL LEVELS IN ORGANIZATION OF VERTEBRATES

MOURER-CHAUVIRÉ C

NEW DISCOVERIES OF EOCENE AND OLIGOCENE BIRDS IN THE "PHOSPHORITES DU QUERCY", FRANCE: THE IDIORNITHINAE (RALLIFORMES, CARIAMIDAE)

PRELIMINARY REPORT ON PLIOCENE/PLEISTOCENE BIRDS OF
EAST AFRICA

Pierce Brodkorb

Department of Zoology, University of Florida Gainesville,
Florida 32611, USA

The present avifauna of Africa is very well known, but in regard to avian paleontology it is still the Dark Continent. But in the East African countries of Tanzania and Ethiopia, where the last 4 million years' history of human evolution is preserved, anthropologists have collected very many fossil birds.

The most extensive material is from Olduvai Gorge in Tanzania, where the Leakeys have collected many thousands of bird fossils, ranging in size from ostrich to tiny passerines, and extending back through about the last 2 million years. At nearby Laetolil the avian record is nearly 4 million years old, but is principally only of egg shells and tracks of gallinaceous birds in the volcanic deposits that include bipedal human footprints.

The Ethiopian fossils were collected by the International Hadar Expedition and the International Omo Expedition, under French and American auspices. The age of the Ethiopian birds is similar to that of the oldest Olduvai material, and to the Laetolil tracks and eggs, thus giving identifiable bones back nearly 4 million years.

Half a century ago a few specimens from Olduvai Gorge were sent to the British Museum and have been reported by Lowe (1931) and by Harrison and Walker (1976, 1979). The other Olduvai birds and those from Ethiopia are under study at the University of Florida. I am greatly indebted to F. Clark Howell, D.C. Johanson, Y. Coppens, and their associates for the opportunity to study the Ethiopian fossils, and particularly to Mary D. Leakey who carefully collected most of the Olduvai material, and who has helped in so many ways. Many students at the University of Florida have helped in preparation and sorting the specimens during preliminary stages of the project. The L.S.B. Leakey Foundation and the Avian Paleontology Fund gave financial assistance.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The localities under study lie along the East African Rift, which extends from the southern end of the Red Sea along the Awash and Omo rivers of Ethiopia to Lake Turkana, and thence south to the Serengeti Plain in Tanzania, where Olduvai Gorge is located.

The Hadar birds were collected in the valley of the Avash River. It arises in the Ethiopian Highlands and flows northeast to empty in the Afar Depression near the Red Sea.

The Omo River also rises in the Ethiopian Highlands. It flows southwest to empty into the north end of Lake Turkana near the Kenyan border.

The Kenya Rift continues southward to the East African lakes and to the Serengeti Plain, on which Olduvai Gorge is located.

All these areas lie in a region of great volcanic activity, from the late Tertiary to the present. The volcanic deposits have been of great value in accurately dating the age of the fauna and flora.

The geology of the Ethiopian localities is summarized by Taieb, Johanson, Coppens, and Aronson (1970) for the Awash area, and by Brown, de Heinzelin, and Howell (1970) for the Omo basin. The geology of Olduvai Gorge is treated in detail in Richard Hay's volume (1980).

The Hadar Formation lies in the Awash Valley of the Afar sedimentary basin. It has an age of about 3 million years.

The Omo Basin beds have four formations, but so far only the two younger ones have yielded bird remains. They are the Shungura Formation with K/Ar dates from 3.75 to 1.84 m.y., and the Usno Formation with age of 3.1 to to about 2 m.y.

Olduvai Gorge is divided into six formations, but birds have been collected only in the lowest two, Bed I with ages similar to those of the Ethiopian sites, and Bed II with dates of 1.7-0.7 m.y.

This part of East Africa is quite arid today in the valleys and on the Serengeti Plain. The grassy plain is broken by scrubby bushes and thorn trees.

At Olduvai Gorge climatic data have been kept over a period of years. The mean annual temperature is 22.8° C, with mean annual minima and maxima of 16.3° and 29.9°C. The mean annual rainfall is 566 mm. During 3-6 months of the year no rain at all falls. The wind on the plain blows most of the time, from the east, at an average velocity of 12.4 kph. As the ground temperature greatly exceeds the air temperature, the evaporation rate is high. The streams in the Olduvai area are intermittent, and in some years there is no flow at all.

In the Pleistocene there was a lake in the Gorge, so the precipitation must have been greater. This is confirmed by the sediments and by the fossils of aquatic plants, invertebrates, fishes, a great many aquatic birds, particularly in Bed I, the lowest formation.

THE FOSSIL AVIFAUNA

This section briefly treats the families of birds that we have thus far identified in the Awash and Omo basins and at Olduvai Gorge.

Family Struthionidae (Ostriches): Struthio sp. incert. A few fragmentary bones occur in the lower part of Olduvai Bed I, and pieces of egg shell in some localities of the upper part of Bed II. Lowe (1933) examined a few scraps of a pelvis from an unknown locality in Bed I, and said "The only way in which they differ is in ... larger size than any Recent Ostrich - not much larger, it is true than the Ostrich from Nigeria in the British Museum". He proposed "the name Struthio oldawayi solely for the convenience of reference". Ostriches show great sexual dimorphism in size, and all of Lowe's comparative material was unsexed. Many fossil ostriches have been named, and it is preferable to regard Struthio oldawayi as a nomen vanum.

Family Podicipedidae (Grebes): Podiceps cf. ruficollis occurs in the Hadar and at several localities in Olduvai Beds I and II. A medium-sized species is also present.

Family Anhingidae (Anhingas): Anhinga hadarensis Brodkorb and Mourer-Chauviré (1982) is the apparent ancestor of the living African A.rufa, but it also shows some similarity to the American species, A.anhinga. It is present in four localities of the Hadar and Omo beds and in three localities at Olduvai Gorge. The age span is from 1.7-3.1 million years b.p.

Family Phalacrocoracidae (Cormorants): Phalacrocorax n. sp. is the most abundant species at Olduvai Gorge, being represented by more than 1.000 specimens of 86 minimum number of individuals, from the lower part of Bed I. The type of Phalacrocorax tanzaniae Harrison and Walker (1979) is from an unknown level and locality; it is perhaps related to the living Indian cormorant Ph.fuscicollis. In Bed II the two living species P.carbo and P.africanus are represented by a very few bones.

Family Pelecanidae (Pelicans): Pelican bones are rare at Olduvai. A small species resembling Pelecanus rufescens occurs in Bed I, and a large species resembling P.onocrotalus in Bed II. Harrison and Walker (1976) described a pelican which may represent one of the above species.

Family Phoenicopteridae (Flamingos): A large species (Phoenicopterus cf. roseus) occurs in Beds I and II at Olduvai. A small species (Phoeniconaias cf. minor) is present at one locality of Bed II.

Family Ardeidae (Hérons): In the lower Olduvai deposits several undescribed species of herons occur, including a cattle egret (Bubulcus), a small Egretta, and an Ixobrychus. In the Omo (age 1.94 million years) Ardea howardae Brodkorb (1980) is larger than all living herons except A.goliath.

Family Balaenicipitidae (Shoe-billed Stork): A specimen from Olduvai I is possibly related to the living Balaeniceps rex.

Family Ciconiidae (Storks): The genera Ibis and Leptoptilos occur. The latter is represented by a giant species and one of more normal size.

Family Anatidae (Waterfowl): Waterfowl are very numerous in the Omo and in Bed I of Olduvai, with many species ranging in size from Spur-winged Goose (Plectropterus) to tiny teal. In Bed II Anatidae are very scarce, as a result of the drying up of the suitable habitat.

Family Accipitridae (Diurnal Birds of Prey): This family is exceedingly rare, being represented by a single species in Bed I and another in Bed II.

Order Galliformes (Gallinaceous Birds): Several species of Francolinus occur in the Omo and Olduvai. Some localities in Bed I have quail (Coturnix).

Family Rallidae (Rails): Rails of several species are abundant in Bed I, from the top to the bottom. None occur in Bed II.

Family Gruidae (Cranes): Only a few bones of crane occur.

Order Charadriiformes: This largely aquatic order is represented in Olduvai Bed I by many hundreds, perhaps thousands, of bones belonging to 7 or more families (Jacanidae, Rostratulidae, Charadriidae, Scolopacidae, Recurvirostridae, Glareolidae, and Laridae).

Family Columbidae (Doves): Dove bones are known only from the middle and upper layers of Bed I.

Family Psittacidae (Parrots): A few specimens of Agapornis occur in two sites of Bed I.

Family Cuculidae (Cuckoos): Only a single bone has been found so far.

Family Tytonidae (Barn Owls): Three bones in the "Zinjanthropus" level.

Family Strigidae (True Owls): Only a few specimens.

Family Apodidae (Swifts): Two specimens only.

Family Coliidae (Mouse-birds): Colius near affinis in Bed I.

Family Alcedinidae (Kingfishers): Bed I only.

Family Coraciidae (Rollers): One bone, Bed I.

Family Upupidae (Hoopoes): Upupa n.sp., Bed I.

Family Picidae (Woodpeckers): Two sites only.

Order Passeriformes: Some 2.000 elements of this order have been segregated so far, and at least 9 families are present, namely: Hirundinidae, Corvidae, Sturnidae, Muscicapidae, Turdidae, Sylviidae, Nectariniidae, Fringillidae, and Ploceidae.

CONCLUSIONS

Among the Pliocene and Pleistocene avian fossils of East Africa that have so far been sorted to the family level or finer there are representatives of 18 orders, 32 families, 44 genera, and 54 species of non-passerine birds. Among the Passeriformes there are at least 9 families, 9 genera, and 11 species - probably many more. Thus at the present time the collection contains a minimum of 19 orders, 41 families, 53 genera, and 65 species. This total will very likely increase as the study progresses.

Although few groups have been studied in depth as yet, it is possible to see some general trends.

1. During the period 3.75-1.8 million years ago the avifauna of the Hadar and Omo (Ethiopia) and of Olduvai Gorge Bed I (Tanzania) included both extinct lineages and lineages ancestral to the modern avifauna.

2. During most of the 3.75-1.8 m.y. period water birds were very abundant, but toward the end of that period there occurred temporary intrusions of a few species of seed-eaters and other birds that occupy drier environments.

3. During the period 1.7-0.7 million years ago, the avifauna of Bed II in Olduvai Gorge was composed of lineages ancestral to the modern avifauna, as far as is known.

4. During Olduvai II time water birds became increasingly scarce, and birds of xeric environments relatively more abundant in the change to today's arid conditions.

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THE EVOLUTION OF PARENTAL CARE IN BIRDS WITH REFERENCE
TO FOSSIL EMBRYOS

Andrzej Elzanowski

Uniwersytet Warszawski, Zakład Paleontologii, Warszawa, Poland

It has been hardly ever denied that the precocial mode of development is primitive for birds, but only Portmann (1938, 1955) and Kramer (1953) made a more specific statement, based on the comparison with recent reptiles, that the earliest birds were superprecocial as are the megapodes (Megapodiidae). This hypothesis has been recently confirmed by the discovery of embryonic skeletons in the Upper Cretaceous of the Gobi desert. Most probably, the Gobi embryos represent a primitive grade of avian evolution. In striking contrast to the modern birds, they have the shoulder and wing skeleton highly ossified, the bones of more advanced specimens being almost complete (Elzanowski, 1981). This indicates that the hatchlings were able to fly as are those of the megapodes (Frith, 1962; Clark, 1964). The superprecocial condition of primitive birds implies that the rise of birds was being accompanied by a significant increase in the energy requirements of embryonic development. This is a crucial point of the presented theory.

INCREASE OF THE ENERGY COST OF EMBRYONIC DEVELOPMENT

A certain degree of endothermy is a necessary condition of the powered flight and, therefore, endothermy had in all probability preceded the powered flight in the evolution of birds; moreover the present evidence is strongly suggestive that Archaeopteryx was endothermic (Ostrom, 1980). Resting and maximal levels of oxygen consumption of endotherm vertebrates are known to exceed those of ectotherms by an average of five- to tenfold (Bennett, Ruben, 1979) and, therefore, if the hatchlings were to fly, the advanced embryos of early birds must have achieved the endothermic levels of metabolism.

The next increase in the energy cost of embryonic development was imposed by the acquirement of flight which is one of the most intricate and demanding means of vertebrate locomotion (Ostrom, 1974). In contrast to the terrestrial locomotion, any flight is an all-or-nothing activity which requires a control of movements in tridimensional space and a high minimal speed; and the powered flight requires also a minimal frequency of wing movements which was probably high in primitive birds (Savile, 1957). Thus, it is easy to demonstrate, that the powered flight requires an almost full efficiency of all basic functions including respiration, thermoregulation, circulation, perception and nervous coordination (Maynard Smith, 1952). Then, if the hatchlings of earliest birds were to fly, they must have approached an adult condition as do the hatching megapodes.

Flight apparatus works as a second locomotory system in birds and, therefore, could not develop at the expense of the pelvic appendage as it did in pterosaurs and bats. On the other hand, the mechanics of flight imposes extremely high strength requirement on the pectoral appendage which makes its development very expensive. All major forces acting on the wing are perpendicular to its axis and tend to break and dislocate the bones. To ensure a sufficient safety factor, the bones have to be highly ossified and the joints

protected by ligaments and special bony supports (the external condyle of the ulna and the internal labrum of the carpometacarpal trochlea). Because of all these demands, the flight apparatus has to be almost complete before the onset of flying and, therefore, its development is very expensive if the chicks are to fly soon after hatching; for this reason (Ricklefs, 1973) the development of flight is delayed in modern birds, except for the megapodes.

The increase of the energy cost of embryonic development caused a proportional increase of the energy expenditures for egg formation which placed a tremendous strain on the female as it does even in the modern precocial birds (King, 1973; Ricklefs, 1974; Murton, Westwood, 1977; O'Connor, 1977; Maxson, Oring, 1980) although the latter have significantly reduced the cost of egg formation by hatching at an earlier stage and retarding the development of wing.

If the energy resources are limited, egg size can be maintained only by increasing time taken for the formation of one egg - which rapidly becomes inefficient - or by decreasing the frequency of laying (King, 1973; Murton, Westwood, 1977). It is therefore reasonable to expect that the females of earliest birds could lay the eggs only at long intervals as do the megapodes.

The reproductive consequences of superprecociality are best illustrated by the recent magapodes. The magapode eggs are very large (10-17% of the females body weight) and rich in yolk which constitutes from 50% (in Leipoa ocellata and Alectura lathami) (Vleck et al., 1980) to 62% (Megapodius freycinet) (Meyer, 1930) of the egg weight. In the total energy content of the egg, the megapodes are surpassed only by the kiwis (Apteryx spp.), which, however, lay very small clutches of 1-2 eggs in the wild (Reid, Williams, 1975). The laying intervals are very long and irregular depending on food resources, e.a., 4-21 days in Leipoa ocellata (Frith, 1962), 9-20 days in Megapodius reinwardt (Crome, Brown, 1979). Although the incubation period is very long e.a., 50-96 days in Leipoa ocellata (Frith, 1962), the metabolic rate of embryos appears to be higher than that of other birds (Seymour, Ackerman, 1980). The magapodes cover a size range of 0.6-2.0 kg and thus appear to be on the average somewhat larger than the primitive birds (Archaeopteryx, Gobipteryx, Ichthyornis), the maximum weight estimate of Archaeopteryx being 0.5 kg. Therefore, in the primitive birds the impact of the energy cost of egg formation on the female was probably even stronger and in any case not weaker than in the megapodes.

EARLY EVOLUTION OF PARENTAL ROLES

An energetic limitation of laying rate means an energetic limitation of fitness and implies a strong selection pressure to improve the female's energy budget. The female should be then delivered from any activities other than feeding and laying. I propose that at this stage the male assumed the care of eggs.

There are essentially only two modes of incubation that could be practised by the earliest birds: the eggs may have been incubated at the surface, as in most-ground living birds, or they may have been buried as in the magapodes and many reptiles (including all crocodiles and most medium to large sized, leg-propelled representatives of other groups).

If the eggs have been still buried, then the successive laying would require the repeated digging for deposition of each egg. Such a nesting mode, best illustrated by the magapodes, is extremely time- and energy-consuming, and the megapode male often assumes the heavier tasks. In the Scrub fowl (Megapodius freycinet) and other species of this genus, and the Maleo (Macrocephalon maleo) both members of a pair are known to work by the deposition of eggs and, in some Megapodius populations, also by the mound-building, but detailed observations of the Orange-footed scrub fowl (M. reinwardt) have shown that the female tends to turn heavier tasks over to the male (Crome, Brown, 1979). In the Brush turkey (Alectura lathamii) the male builds the mound and regulates its temperature alone but does not help the female to place the eggs; however the female's digging in the mound, built mainly, as it is, of leaf material, seems to be not a very heavy task as compared to digging in the ground. Talegallus spp. and Aepyodius spp., which also occur in dense jungle and build the mounds of vegetable remains, have probably similar breeding habits (Frith, 1968). The parental investment is certainly the greatest in the male Mallee fowl (Leipoa ocellata) which inhabits unproductive, arid areas; the male does almost all work at the mound, including building, temperature regulation and digging for egg deposition (Frith, 1962).

If the eggs of earliest birds were left on the ground, they would be strongly endangered by predators and subject to the temperature fluctuations. These and possibly also other factors (an excessive dehydration might have been also important if the habit of surface incubation were of recent origin) raised an urgent need, whenever the surface incubation evolved, to conceal and to heat the eggs, both functions being performed by the habit of brooding the clutch. Brooding requires little energy but much time and this precludes effective feeding which was necessary for the production of further eggs. It appears therefore that the male care of eggs was very likely to evolve as a response to the rise of the energy cost of egg formation.

The above conclusion clearly challenges the almost unquestioned view that the biparental care is primitive for birds (Kendeigh, 1952; Selander, 1972; Jenni, 1974; White, Kinney, 1974; Skutch, 1976). An argument invariably given in support of this view is the overwhelming predominance of biparental care among living birds; but in fact this applies only to the neognathous birds, among which the male assumed all parental duties only in a few small and taxonomically isolated taxa (Kendeigh, 1952; Jenni, 1974; Skutch, 1976); some of these cases may ultimately prove to be primitive, but most of them, especially among the Charadriiformes, are clearly secondary and can be explained with reference to local conditions (Wittenberger, 1979) as food supply (Graul et al., 1977; Bergstrom, 1981) or predation (Maxson, Oring, 1980). Unexplained, however, has been a striking fact, that among 56 species of palaeognathous birds, living in habitats as diverse as possible for terrestrial birds, in 55 species all parental duties are performed by the male (Kendeigh, 1952; Meise, 1963). In light of the present argument and taking into account a good evidence supporting the old view that the tinamous and ratites are the most primitive among living birds (Gingerich, 1976; Simpson, 1980; Houde, Olson, 1981; McGowan, 1982), I suggest that the male parental care of palaeognathous

birds is a primitive mode inherited from the early stage of avian evolution. Contrary to recent claims (Meise, 1963; Cracraft, 1974) the parental care should not be used as evidence in support of the monophyly of Palaeognathae.

In the rheas (Rhea americana and Pterocnemia pennata) (Bruning, 1974; Davies, 1976) and at least two (and probably more) species of tinamous (Lancaster, 1964; Jenni, 1974) the males are simultaneously polygynous and the females are sequentially polyandrous (Wittenberger, 1979); the male accepts eggs, which are fathered by him, from several females who lay concurrently, and the female deposits her successive clutches to the nests of several males. The sequential polyandry alone occurs in the Variegated tinamou (Crypturellus variegatus) (Beebe, 1925) and has been also observed in the captive Emu (Dromaius novaehollandiae) (Davies, 1976) and one wild female of the Australian cassowary (Casuarus casuarus) (Crome, 1976). The polygyny alone occurs in the Highland tinamou (Nothocercus bonapartei) (Schäfer, 1954). The main advantages of the polygynous/polyandrous system are (Lancaster, 1964; Davies, 1976; Maynard, 1977): (1) a shortened period of laying into one nest, which facilitates the timing of development and hatching, and reduces the losses from predators; (2) a significant increase of the number of eggs, both those fathered by one male in his nest, and those deposited by one female per season. Thus the polygynous/polyandrous system is clearly an adaptation compensatory for the disadvantages of protracted laying intervals. I suggest that it evolved after the male had assumed parental duties but the cost of egg formation was still high and the laying intervals were long.

BIPARENTAL CARE

Once the parental care had been assumed by the male and subsequently improved, especially by the development of an efficient parent-offspring bond, the young could hatch at earlier stages with a retarded flight apparatus. A primary selective factor promoting the earlier hatching acted probably to increase the survival of young, since precocial chicks guided by a parent are much safer than a clutch lying on the ground. Subsequently, the earlier hatching allowed the female to lay eggs with a smaller energy content and, thereby, to improve her energy budget. Moreover, the wings have been no more necessary immediately after hatching and their development could be retarded what made possible a further reduction of the energy expenditures for egg formation. Once the female was delivered from the stringent energy limitations she was very likely to assume a share in the more and more elaborated parental duties, because eggs and precocial chicks, especially when numerous, are certainly better cared for by two than by one parent (Lenington, 1980). Therefore, and contrary to the hitherto accepted views (Kendeigh, 1952; Selander, 1972; Jenni, 1974; White, Kinney, 1975; Skutch, 1976), the biparental care is very likely to have evolved more than once among birds.

The biparental mode prevails among the neognathous birds and occurs in a single palaeognathous species, the Ostrich (Struthio camelus) which had been thought by Kendeigh (1952) to have the most primitive breeding system among the Palaeognathae. In fact, the breeding system of the Ostrich is, I believe, a secondary modification of the polygynous/polyandrous system of rhea type, which cannot be primitive in any sense. The female (at least in S.c.massai-cus) drifts through the territories of several males and mates with them

(Bertram, 1980); the male mates with many females (up to five) who lay the eggs into one nest (Sauer, Sauer, 1966; Bertram, 1980); but both incubation and care for young are shared by the major (dominant) hen, who chases away the other (subordinate) females before hatching of the young (Sauer, Sauer, 1966). I suggest that the biparental care of the Ostrich evolved in response to the heavy egg predation which began with the late Tertiary appearance of the canids and hyaenids in Africa (Savage, 1978); even now, with great parental contribution from the female, the predation rate on nests is very high and exceeds 75% in S.c.massaicus (Bertram, 1980). If the male were unaided and the nest had to be left unguarded, the predation rate would be catastrophic, and the female would gain little by laying eggs for many males because nearly all nests would be destroyed; but she would gain by preventing the eggs from being left unattended. Other ratites live in areas (South America and the Australian region) which have no comparable sets of predators, and, moreover, the Ostrich breeding system appears to be of recent origin in being conspicuously variable and unbalanced even within one wild population (Sauer, Sauer, 1966).

I thank Dr. R.Seymour (University of Adelaide) for the comments.

SUMMARY

Embryonic bird skeletons, recently described from the Upper Cretaceous of Gobi (Elzanowski, 1981), confirmed an old view (Portmann, 1938, 1955; Kramer, 1953) that the earliest birds were superprecocial i.e., their hatchlings were able to fly. This implies that the rise of birds was being accompanied by an increase of the energy requirements of embryonic development and a proportional increase in the energy cost of egg formation, which resulted in the successive laying of a clutch with long laying intervals. This raised a strong selection pressure forward the male care of eggs since the female should be free from any duties other than feeding and laying. The male parental care appears then to be a primitive condition which has been retained by the palaeognathous birds.

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THE MORPHOLOGICAL EVIDENCE FOR RATITE MONOPHYLY:

FACT OR FICTION

Alan Feduccia

Department of Biology, University of North Carolina,
Chapel Hill, North Carolina 27514, USA

INTRODUCTION

During the past century one of the most disputed problems in avian systematics has been the relationships of the ratites to other birds and to one another. T.H. Huxley (1867) set the stage for all subsequent studies of ratite evolution with his study of the avian palate. Huxley envisioned the ratites as ancient relicts of a once great evolutionary radiation: "Though comparatively few genera and species of this order now exist, they differ from one another very considerably, and have a wide distribution... Hence, in all probability, the existing Ratitae are but the waifs and strays of what was once a very large and important group" (1867, p. 419). Huxley divided all living birds into two groupings, the Ratitae, which contained the large flightless ratites and the kiwi; and the Carinatae, which accommodated all other birds. Yet, Huxley was perplexed by the tinamous, which although possessing the "dromaeognathous" (=paleognathous) palate, had a sternum typical of the Carinatae. Ever since Huxley's era, the question of ratite affinity, although taking on various types of argumentation from time to time, including some of the most bizarre zoogeographical proposals, has focused primarily on the palate. Recently, several other characters have come into the picture, and studies of biochemical systematics have been accomplished. The history of the controversy has been skillfully summarized by Sibley and Ahlquist (1972), and recently updated by Sibley and Ahlquist (1981) in their paper describing DNA-DNA hybridization studies. In this paper I do not intend to attempt to evaluate all of the data now available to formulate an **eclectic view of ratite** relationships, but rather to critically examine the strictly morphological characters thought to be "derived" that have been used to unite the ratites into a monophyletic assemblage (Cracraft, 1973; 1982a). Because the proper allocation of fossils depends on the recognition of characters that unequivocally identify taxa it would seem particularly appropriate at this time to reconsider the key characters of ratites.

KEY RATITE CHARACTERS

As this paper will only be concerned with strictly morphological characters, we need only consider the structure of the ramphotheca, the large ilioischiatric fenestra and the paleognathous palate.

In each case authors have considered the respective characters involved to be indicative of a monophyletic ratite assemblage that included the tinamous as the sister group. The basic question with all three characters has not to do with their occurrence within the ratites, but whether or not they are primitive or derived. Also, because so many morphological features of ratites are neotenic (see de Beer, 1956; Feduccia, 1980) one must also ask if these same characters are indeed neotenic and, if so, how should neotenic

characters be interpreted for purposes of systematics. Let us then, briefly consider these three characters.

Parkes and Clark (1966) argued that a peculiar rhamphothecal structure possessed by all of the ratites and tinamous indicated that they were most likely related to one another. They described the character as follows (p. 461): "The culmen is an elevated, flattened ridge which usually widens (except in kiwis) near the tip of the bill. At the base of the culmen is a cere-like structure, the anterior margin of which is U- or V-shaped, with the point toward the forehead. The lateral margins of this structure extend as distinct grooves... "On the lower mandible, the rhamphotheca appears tripartite." They noted considerable variation in the ratites and tinamous, but concluded that the structure exhibited a consistent pattern within these birds. There are several problems with the use of this character to indicate ratite monophyly. The most difficult is that these structures do not differ in any meaningful detail from the rhamphothecal segmentation found in the Procellariiformes and Pelecaniformes.

In order for these features to be used as a shared derived character to indicate monophyly of the ratites, it must be clearly demonstrated that the character was derived but once in a supposed tinamou-ratite assemblage. It is currently impossible, without a thorough knowledge of the development of the rhamphotheca in ratites and in other birds that possess them, to establish that the tripartite structure is truly homologous from one group of the ratites to another. It should be pointed out here that even Parkes and Clark (op. cit.) did not feel as strongly about the rhamphothecal characters as did Cracraft (1973). As they state of ratites (p. 469): "Their monophyly is thought to be at approximately the family level, with several lines of descent from a family of "proto-tinamous" having independently attained the "ratite grade".

Leaving the discussion of the most complicated character, the palate, until last, we may now consider the only other character thought to be a shared, derived character indicating ratite monophyly. This character is the open ilioischiatric fenestra that Cracraft added in 1974. To be brief, the ilioschiatic fenestra is clearly neotenic in birds (Olson, 1973; Feduccia, 1980) and almost certainly primitive, and is therefore of no use in ratite systematics. One should note here that although Cracraft readily uses neotenic characters as shared, derived characters (Cracraft, 1982, p. 689), this procedure is open to criticism. Because so many features of ratites are neotenic as shown by their occurrence in the embryos of other birds, we must now pause to consider the use of neotenic characters in systematics.

The basic question before us is what information do neotenic characters have in phylogenetic reconstruction? Cracraft (1981; p. 689) is quite emphatic in his belief of their importance when he states of ratites that, "... an argument of neoteny is a prima facie admission that the similarities in question are derived and not primitive, that is, the adult condition of the ancestor is "replaced" in the descendant by the juvenile condition... "Yet other authors, particularly Hecht and Edwards (1974) feel that such characters must logically carry an extremely low information content... "The use of such character states as shared and derived characters is placing undue weight

on such complexes, since they do not preclude parallelism. In fact, in such characters, parallelism should occur frequently, since the necessary genetic changes are minimal and the morphological changes maximal." (Hecht and Edwards, 1976a: 656). In the case of the ilioischiatric fenestra most birds have the ilium and ischium broadly fused; in ratites the fusion does not take place and therefore the bony connection is lost. Other characters that represent loss are reduction or loss of the keel of the sternum and the reduction in size of the wing elements, both of which Cracraft (1974) used as shared, derived characters. As Hecht and Edwards (1976) have warned, such characters that represent loss or over simplification through neoteny have zero information content. Following Cracraft's use of neotenic characters as shared, derived features, we might logically include all flightless rails in the same genus as they all possess reduced wings, a keel-less sternum and an open ilioischiatric fenestra (Olson, 1973); all extinct flightless geese could be treated likewise.

We see then that postcranial characters supporting ratite monophyly are totally lacking. Clearly, the critical question concerning the use of morphological features in defining the ratites revolves around the paleognathous palate alone. Is it a primitive feature of birds, or derived from neognathous birds, possibly through neoteny?

Sam McDowell (1948; following de Beer, 1956), considered the paleognathous palate of ratites to be so variable as to defy definition. Following McDowell, Alexander Wetmore (1951) combined the two major subclasses of living birds - the Paleognathae and the Neognathae - into a single group, and most recent **classifications** have followed this course.

McDowell recognized four types of paleognathous palates (with a possible fifth type reserved for the imperfectly preserved elephant-birds). These included the tinamiform type, for rheas and tinamous; the casuariiform type, for cassowaries and emus; the struthioniform type, for the ostrich; and the apterygiform type, for the kiwi. Obviously, McDowell **did not feel that the** palate could be used as evidence for a monophyletic ratite assemblage, and in fact, he felt that the ratite palate could be the result of arrested development as other features of the ratite skull are so derived (e.g., sutures retained in skull). McDowell also made the important point that where neoteny is known to have affected a particular part of an organism, one usually sees similar effects in other parts. It is a difficult task to arrest development to accomplish a specific goal (e.g., loss of flight apparatus), while allowing all other features of the organism to develop to the full adult state. "Perennibranchiate" amphibians which retain the external gills through neoteny so they can persist in an aquatic environment, also retain neotenic skull and muscle characters.

Walter Bock (1963), who considered the palate definable, thought that it indicated a common origin of all ratites and tinamous, but was not primitive in living birds. He believed that the paleognathous palate was derived from the modern neognathous palate. He stated (1963, p. 53) that "the ratites do not appear to be primitive among birds... nor do they have to be any older than other typical avian orders".

Since these papers have been published, two notable fossils have been discovered that cast considerable light on this problem. Gobipteryx, described by Elzanowski (1976) from the Cretaceous of central Asia and other paleognathous volant birds from the early Tertiary of North America described by Houde and Olson (1982) strongly suggest that indeed the paleognathous palate is primitive within birds. Claims that Hesperornis was paleognathous (Gingerich, 1976) are not well established, primarily owing to problems of homology, as Hesperornis is so different from all other birds.

It should be pointed out here that although I personally consider the discovery of paleognathous birds from the Cretaceous and Paleocene as evidence that the paleognathous palate is most likely primitive within birds, cladists would not interpret the fossil palatal information the same way. For example, although the open ilioischiatric fenestra is present in Hesperornis and Ichthyornis (as well as Archaeopteryx), Cracraft (1982) considers the condition to be a secondarily derived character in these birds. In order for these birds to conform to the monophyletic scheme for Hesperornis, loons and grebes, the teeth in Hesperornis and Ichthyornis are postulated to be (p. 54), "... atavistic manifestations of development". Thus, Hesperornis evolved teeth from a toothless ancestor! Obviously evolutionary systematists and cladists are on such different wavelengths at present that there is little room for any meaningful discussion between the two schools of thought.

Finally, if the paleognathous palate is primitive within birds, as the fossil record indicates, is it also a condition found in the early development of neognathous birds as one might expect? This has been reported to be the case (Pycraft, 1900; Jollie, 1958), but the evidence is sketchy and no substantial evidence has been marshalled to support the occurrence of a truly paleognathous palate in the embryos of neognathous birds. One might more realistically look for certain key features of the paleognathous palate in the embryos of neognathous birds, and as Cracraft (1982) (p. 688) points out: "Perhaps the most important characteristic of the paleognathous palate ... is the typically strong fusion of the pterygoid-palatine-vomer articulation". The fusion of the pterygoids and palatines in ratites has generally been assumed to be a condition derived from neognathous type because most embryological studies of the skeleton of birds have been based on Gallus (Jollie, 1957) which in early development shows the pterygoids and palatines as separate bones. However, Gallus is a difficult bird to use for studies of the early embryology of the skeleton because gallinaceous birds are so precocious that development of the skeletal architecture takes place very early. I have begun a massive study of the early embryology of the avian skeleton and can report, at least provisionally, that indeed a single primordial bone that will later give rise to the pterygoid and palatines is present in certain embryos such as Cathartes. Although these observations will require much more additional corroboration, there is certainly a strong preliminary indication that the pterygoid-palatine fusion is primary, and not a derived condition from an originally separate palatine and pterygoid.

From the presently available evidence, the paleognathous palate as a shared, derived character uniting ratites into a strictly monophyletic assemblage cannot be substantiated.

DNA COMPARISONS

This demonstration that the current morphological features used to define ratites are unusable is quite timely in light of the recent paper by Sibley and Ahlquist (1981) who, using the technique of DNA-DNA hybridization claim to support not only a monophyletic "ratite" assemblage, but also a specific phylogeny within the group. These recent biochemical studies such as the one cited above and those of Feeney and Allison (1969), Prager and co-workers (1976), as well as studies on karyotypic structure (de Boer, 1980) all arrive at the conclusion that the ratite assemblage is monophyletic, yet it is characteristic of these studies to begin with the implicit view that the group is most probably monophyletic so that extensive out group comparisons are not accomplished to the degree that would be desirable. It should here be noted that de Boer's study of chromosomes may not bear on ratite monophyly because the unique features of the ratite karyotype are also found in crocodilians as well as some other reptiles (see review by Barrowclough, 1981).

I am personally very much impressed with the potential of DNA comparisons within birds accomplished by Professor Sibley, yet all of the results from such studies must ultimately be totally comparable with results of studies of morphology and the fossil record. After all, the phenotype is ultimately a product of the genotype. True, there are cases where organisms with nearly similar genotypes (as reflected by similar macromolecules) are quite different morphologically, a case in point being Man and chimpanzee, but nevertheless there should generally be considerable concordance between morphological and biochemical comparisons if the latter are valid. That biochemical comparisons and more particularly DNA may ultimately resolve many problems of avian systematics should not in the least deter the paleontologist and morphologist from pursuing their studies. DNA comparisons are at an early stage and are certainly not without their problems. Let us not forget the views expressed by Doolittle and Sapienza (1980) and Orgel and Crick (1980) that much of the DNA in higher organisms could be described as "selfish". They argued separately that such DNA has no appreciable phenotypic effect and would function only to ensure its own survival or self-preservation within the genome. There is considerable evidence for this point of view, and if, indeed, a large percentage of the genome turns out to be this "excess" or "incidental" DNA then comparisons of DNA hybridization will certainly be forced to recognize this as a major drawback. With respect to this excessive DNA in the genome, Jain (1980: 648) comments: "Nature places considerable premium on playing safe so that it will not run short of raw material even if this means indiscriminate production leading to sequences which are destined to remain functionless." ... we must be prepared by now to accept some degree of confusion". To what degree this "confusion" will interfere with DNA comparisons within birds is not clear, but it certainly is a signal for extreme caution in wholesale acceptance of results from DNA hybridization alone. If very large amounts of DNA within the genome are not relevant to the production of the phenotype what would one be measuring? There may also be problems of convergence at the molecular level that we may simply not be aware of, and as professor Mayr has warned (1980): "I am afraid we may have to transfer the lesson we have learned from morphological characters also to the molecular characters, or at

least to some of them." We need only remember that hemoglobins of similar molecular structure have evolved quite independently in insects and vertebrates.

Another current problem relates to results of a study of the avian genome undertaken by Burr and Schimke (1980) in which they performed DNA renaturation procedures on single individuals of 12 species representing four orders. They found no correlation among the observed curves, which represent genomic structure, and taxonomic relatedness. As an example, the domestic chicken (Gallus domesticus) and the red jungle fowl (Gallus gallus) have very different melting curves. This paper is reviewed in more detail by Barrowclough (1982). These types of studies indicate at least that much more needs to be learned about the structure of the genome before any wholesale acceptance of DNA-DNA hybridization can be considered.

It is my view, then, that studies of morphology should continue quite independently of biochemical and DNA comparisons, and should certainly never depend on such evidence to define monophyletic assemblages; this should be accomplished independently by the morphology.

THE FOSSIL RECORD

The fossil record has provided very little evidence concerning ratite evolution. It should be apparent from previous discussion that where cranial material, specifically the palate, is not available, there is no basis upon which to assign fossils of large flightless birds to the "ratite" assemblage. Thus the identification of dromornithids (Rich, 1979) and fossils from New Caledonia (Poplin, 1980) as ratites must be considered strictly provisional. We must recall from the lesson of flightless rails (Olson, 1973) that the time involved in the evolution of flightlessness may be extremely brief, perhaps measured more appropriately in generations than in millenia. Also, Pleistocene fossils from Hawaii, a flightless goose (Thambetochen) and a flightless ibis (Apteribis) have shown clearly how bizarre the anatomy of flightless birds can become within one geological epoch (perhaps a few million years). The condition of the goose's wing, sternum, and scapula and coracoid closely resembles those of the large ratites and without the bill the ibis was almost unrecognizable as an ibis (Olson, Wetmore, 1976). In fact, the bones of the hind limb of the ibis were quite kiwi-like! With this in mind, there is no current evidence to preclude the possibility that the moas and elephant birds could have evolved in one geological epoch from volant ancestors. No fossils for either group are known prior to the Pleistocene and there is no evidence that they are any older. Evidence for antiquity of the ostrich (as proposed by Cracraft, 1974) is also totally wanting; in fact, the fossil evidence argues just the opposite (Feduccia, 1980).

SUMMARY AND CONCLUSION

The currently advocated view that the living ratites are cladistically monophyletic (Cracraft, 1974) on the basis of a handful of characters thought to be "derived" rests on extremely flimsy evidence. The large ilioischiatric fenestra and paleognathous palate are almost certainly primitive or neotenic, and the same may well be the case for the rhamphothecall structure. That ratite chromosomes closely resemble those of crocodilians fits the general pat-

tern of the morphological evidence. It should also be pointed out that although Sibley and Ahlquist (1981), and Prager et al. (1976) interpret their DNA and biochemical analyses of ratites to indicate that they are monophyletic, there is nothing in their data to preclude the possibility that the ratites and tinamous are paraphyletic groups derived through successive waves of radiations. Nor is there any evidence that the ratites are truly ancient; some could be ancient and some very recent; some may be primitive forms derived through neoteny and others may be of recent vintage, exhibiting the "classical" ratite suite of characters derived through neoteny.

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LOWER CRETACEOUS BIRDS FROM MONGOLIA AND THEIR EVOLUTIONARY SIGNIFICANCE

E.N. Kurochkin

Palaeontological Institute of the USSR Academy of Sciences,
Moscow, USSR

INTRODUCTION

In the last three decades the understanding of the paths of principal groups of terrestrial vertebrates appearance and historical development has advanced considerably. In many cases a new paleontological information was added concerning the evolution of crossopterygians and dipnoans, labyrinthodonts and mammallike reptiles. The paleontologists testified now on the whole and in details in many situations how the principal groups of amphibians, reptiles and mammals had risen. But the same cannot be mainly said about a birds, largely because of the absence of new data.

The hypotheses on birds origin in general use has been focused mainly on the investigations of the Upper Jurassic specimens of Archaeopteryx. New findings of the Mesozoic Priscavolucris from Spain (Gomez Pallerola, 1976), Wyleyia from Lower Cretaceous of England (Harrison, Walker, 1973), Enantiornithes described as a new subclass from Upper Cretaceous of Argentina (Walker, 1981) need the more careful study, their place among birds is doubtful. Well-known Upper Cretaceous hesperornises and ichthyornises have an unclear systematic position. New investigations of original materials (Martin, 1980) backed up the previous considerations on Hesperornithiformes as a side branch of archaic birds evolution. On the one hand skeleton of Ichthyornithiformes bears the advanced features of true carinate birds, on the other hand it has such archaic morphological peculiarities, as teeth in jaws and amphicelous vertebrae. I think, that ichthyornises cannot be drawn nearer to some recent or known fossil birds, but they present a typical mosaic ancient group of birds as a separate order Ichthyornithiformes in infraclass Carinatae according to P. Brodkorb's system (1963). In Lower Cretaceous two species of Enaliornis are also known in Albian of England, which are the ancient loons (Brodkorb, 1963) or hesperornises (Martin, 1980). On the other hand true birds (Brodkorb, 1976) and paleognathous birds (Elzanowski, 1977, 1981) are found in Upper Cretaceous. But these facts are not able to afford on reasoning about origin of birds on the whole.

Traditionally, Archaeopteryx, being the earliest bird known, was considered to be directly ancestral to modern birds. Some old hypotheses in the new interpretation on the origin of Archaeopteryx from Coelurosauria (Ostrom, 1976) and unexpectedly new which prove that birds, originated from ancient crocodiles (Walker, 1972; Whetstone, Martin, 1979) accepted by numerous paleontologists, especially, by paleoherpetologists, but it was not generally recognized. In my opinion these hypotheses raise more new questions, that settle the old problems. Somewhere a compromise hypothesis was suggested by Tarsitano and Hecht (1980), which argues against the origin of Archaeopteryx from a common archosaurian tree, on pseudosuchian level between Euparkeria and Lagosuchus. But is Archaeopteryx a direct ancestor of birds? One may ask in which meaning it is an ancestral and transitional form, in direct phylo-

genetical sense or as the only form which demonstrates a possible transition way from reptiles to birds by the mosaic combination of characters of separate systems and structures of them, what was going with heterochronias at different times. Therefore, around Archaeopteryx we have two various problems: 1. Origin of Archaeopteryx proper. 2. Was Archaeopteryx a direct ancestor of birds? But there are 4 different hypotheses on the origin of Archaeopteryx: pseudosuchian, ornithischian, crocodilian and theropodian (saurischian). They were analysed enough in detail by L.P. Tatarinov (1980). But Tatarinov did not also raise a question of Archaeopteryx as a direct ancestor of birds. We consider what the birds origin cannot bind up a priori with Archaeopteryx origin. There is a methodological mistake putting an erroneous precondition in any final conclusion. For the present not the attempts, with the exception of Ostrom (1976), to contend that Archaeopteryx is phylogenetically bound with birds. As a rule, the problem is in the following: is Archaeopteryx a bird or a reptile, is it a **transitional form**, from which group of reptiles is it originated? New palaeontological data present come indirect arguments that Archaeopteryx was not a direct ancestor of the modern birds.

From Upper Cretaceous of Mongolia a new theropod dinosaur Avimimus portentosus was lately described. It had a intertarsal articulation, half-fused metatarsus, the third condyle of femur for fibula, and its ulna and carpometacarpus which were constructed by birds type (Kurzanov, 1981). Finding of Avimimus do not support the theropodian hypothesis of birds origin, but quite the reverse it is rather a support for I.I. Shmalgausen's hypothesis on the theropodian dinosaurs origin from Archaeopteryx (1938). Or maybe Avimimus demonstrates that theropods ancestors had that sort of the evolutionary potentials which caused a parallel ways of Archaeopteryx and later theropod extremities modifications? There are two other important Mesozoic findings - Cosesaurus from Middle Triassic of Spain (Ellenberger, 1977) and Palaeopteryx thomsoni from Upper Jurassic of Colorado, USA (Jensen, 1981) presenting pre-Archaeopteryx birdlike animal. At last, there is Ambiortus from Lower Cretaceous of Mongolia.

MATERIAL

This is a partial skeleton of a bird, obtained in 1977 by the paleontologists, headed by A.G. Ponomarenko, from the Joint Soviet-Mongolian Paleontological Expedition. The specimen was found in shales of the lacustrine deposits at Hurilt-Ulan-Bulak locality in central Mongolia, on the northern slope of the Gichgeniyn Nuruu range (Mongolian Altai), about 20 km southwest of Lake Böön-Tsagaan Nuur. The age of these deposits was determined as Neocomian (Hauterivian - Barremian, Unduruhinskaja suite) from the numerous fossil insects and fishes (Zherihin, 1978) or as Hauterivian - Aptian from fossil plants (Krasilov, 1982). Such shallow Lower Cretaceous lake deposits are of wide distribution in this part of Mongolia (Shuvalov and oths., 1975).

The main slab (Figs. 1, 2) contains a partial skeleton of a small bird, the size of a jackdaw (Corvus monedula) consisting of some wing bones, shoulder girdle and vertebrae (proximal half of left humerus, partial carpometacarpus, ulnare, scapula, coracoid, clavicle, fragmentary keeled sternum,

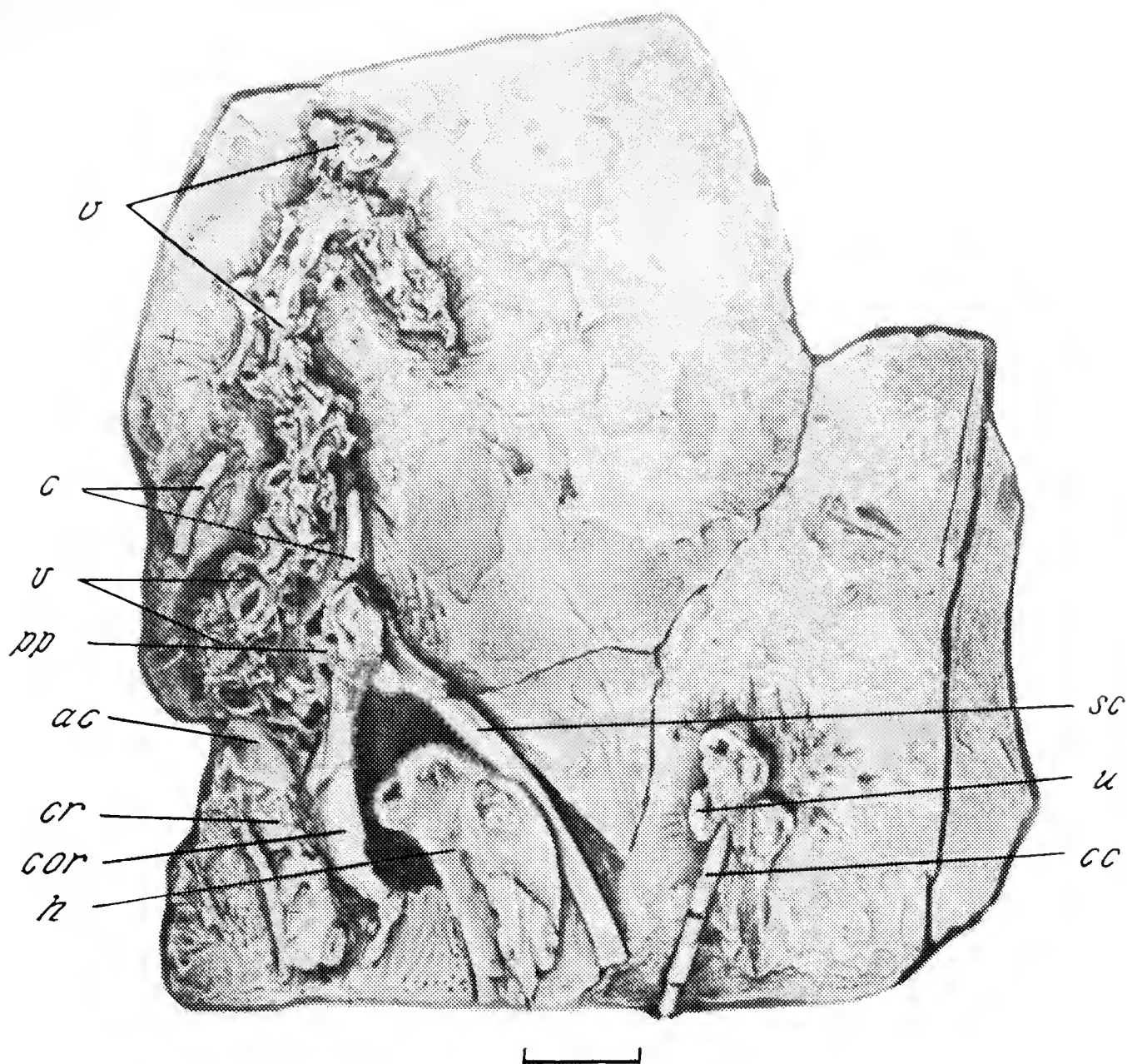


Fig. 1. Ambortus dementjevi (Kurochkin, 1982)

General view of holotype; PIN No. 3790-271+; locality Hurilt-Ulan-Bulak, Bajan-Chongorski ajmak, Mongolia; Lower Cretaceous, Neokomian; ac - apex of carina, c - clavicle, cc - carpometacarpus, cor - coracoid, cr - carina of sternum, h - humerus, pp - procoracoid process, sc - scapula, u - ulnare, v - vertebrae. Natural size

9 to 10 cervical vertebrae, and 3 or 4 thoracic vertebrae (total 14 vertebrae). A smaller associated slab (Fig.3) has the bones, or their impressions, of distal part of a wing: the first, second and third (claw) phalanges of the major digit of the wing, along with well preserved feather impressions.

This bird was described as Ambortus dementjevi (Kurochkin, 1982) and was referred to a new family Ambortidae, and a new order Ambortiformes (Kurochkin, 1982). Because this is a true bird with a keeled sternum and a typically avian shoulder girdle, it was included in the infraclass Carinatae.

Description. Skeleton of Ambortus. Proximal head of humerus lacks a bicipital crest and raised bicipital surface (intumescencia). In place of the sulcus lig. transversus, the only fossa is on the ventral edge of the epiphysis; from this fossa small sulcus leaves out and opens on proximal edge of epiphysis. A fragmentary sternum is delicate and flat, root of a long keel preserved on cranial side of sternum. The clavicles heads have blunt ends and lack clear flattened articulating facets clavicles branches are of the same thickness at full length. Hypocleidum is not developed, but symphysis is well seen on impression. The scapula is narrow and long with a wide articulate humeral facet. A caudal half of saberlike body of scapula has a wide lengthwise groove, placed on the lateral side. The scapular acromion is very distinctive in being produced anteriorly as a long pointed process (pr. uncinatus scapulae), curved at the end ventrally (Fig. 2). Shaft of coracoid is long and narrow,

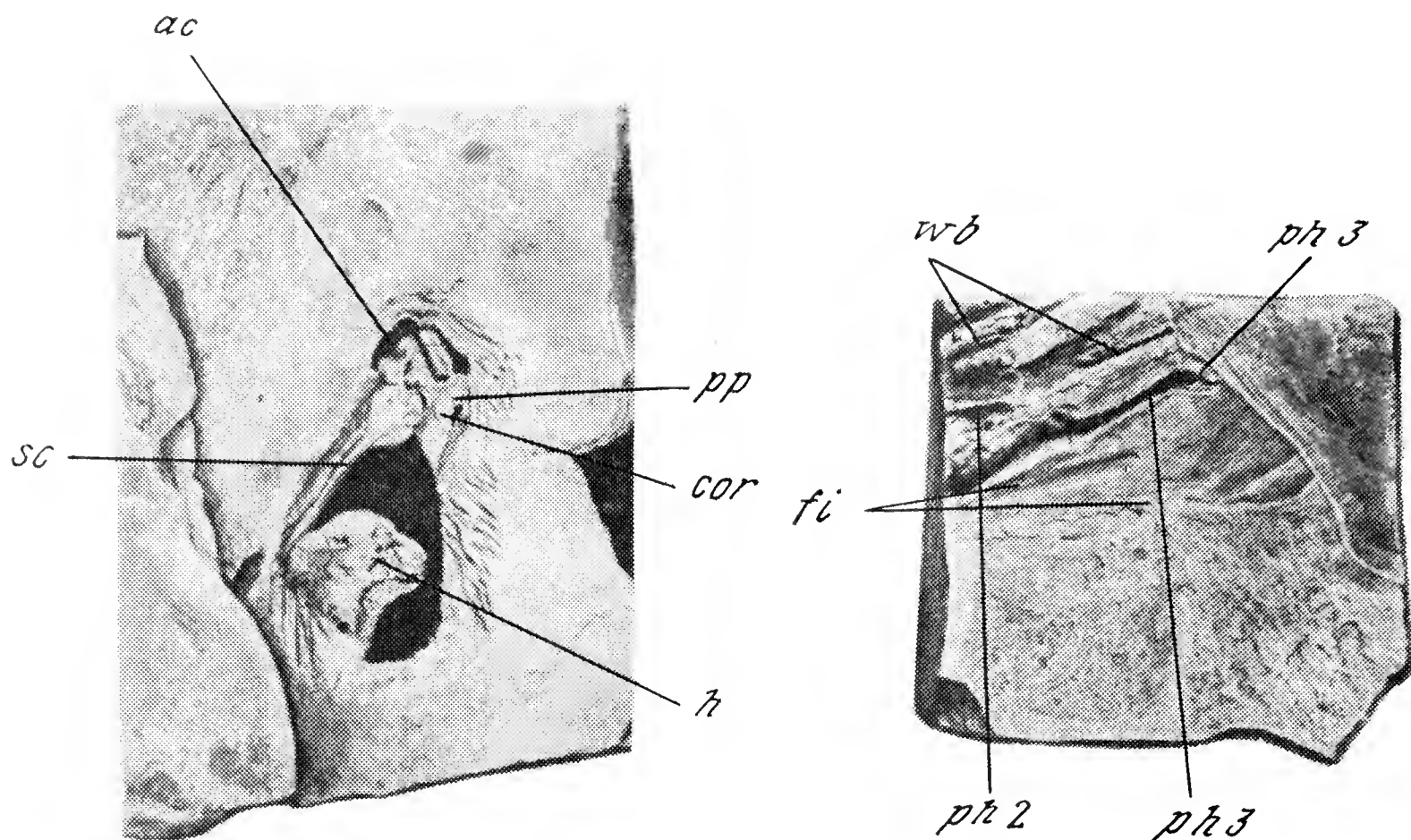


Fig. 2. Head of humerus, coracoid and scapula of Ambiortus dementjevi type specimen, viewed from opposite side; ac - acromion process, cor - coracoid, h - humerus, pp - procoracoid process, sc - scapula. Natural size

Fig. 3. Distal part of wing of Ambiortus dementjevi, PIN No. 3790-272, from the same site; fi - feather impressions, ph 1 - basal phalanx of major digit of wing (impression in matrix), ph 2 - phalanx 2 of major digit (impression only), ph 3 - phalanx 3 of major digit (bone and impression), wb - wing bones (ulna and radius?) and their impressions. Natural size

sternal end of coracoid widened; procoracoid process is wide and flat, near base of this process slitlike foramen is outlined on the cranial side; scapular facet well developed; acrocoracohumeral groove occupies all over the acrocoracoid tip from the caudo-lateral surface; on the craniomedial side, the acrocoracoid has a distinctive lengthwise groove. The carpometacarpus is typically birdlike, fused; process of metacarpal I is fused with a wide apex. Curved ulnare is present in metacarpal joint. The centra of the cervical vertebrae appear to be amphicoelous, particularly from the cranial surface; the transversal section of vertebral bodies and their articulate surfaces are oval stretched dorso-ventrally. Basal phalanx of the wing major digit has the typically bird structure, as well as the second phalanx, but the third one is clawed.

The bones are thin-walled hollow inside on transversal breaking of a humerus, coracoid and carpometacarpus.

General size of A. dementjevi, as stated above, corresponds to modern jackdaw. Full size of most part of bones is unknown, only coracoid is more or less completed, this length is 32 mm.

COMPARISON

The details of the structure of Ambiortus are of three types: (1) generalized features typical for true birds, (2) features held in common with particular groups of fossil and some modern birds, (3) features that are unique

to Ambiortus and require its separation as a new taxon of a high rank.

The features, **shared** with typical birds, as opposed to Archaeopteryx, are: shaft of coracoid long and narrow; sternal end of coracoid wide; acrocoracoid present; scapula long and straplike of typically avian articulation with the coracoid; furcula present; sternum present and keeled; dorsal and ventral tuberculae of humerus present; carpometacarpus fused; curved ulnare in metacarpal joint. These characters show Ambiortus to be an advanced carinate bird with good powers of flight.

The second group of features are those that are probably archaic within the Ambiortiformes. The humerus lacks a bicipital crest and raised bicipital surface, as it is also true of Archaeopteryx, Ichthyornis, and the paleognathous carinate birds recently recognized from the Paleogene of North America (Houde, Olson, 1981). In place of the sulcus lig. transversus, the only fossa is on the ventral edge of the epiphysis, as, for example, in the modern families Gruidae, Anatidae, Upupidae, and Momotidae. The ends of the furcula lack flattened articulating facets, thus being similar to Archaeopteryx and the Paleogene paleognathous carinates. The scapular acromion is very distinctive in being produced anteriorly as a long pointed process similar only to the Paleogene paleognaths. This process, probably, serves to strengthen the clavicular-coracoidal articulation. The acrocoracoid has a wide and short impressio lig. acrocoracohumeralis, as in the Tinamiformes and Paleogene paleognaths. On the cranio-medial edge, the acrocoracoid has a distinctive lengthwise groove. A similar structure can be seen in modern Gruiformes and Strigiformes and is especially well developed in the Alcedinidae and Momotidae. The Paleogene paleognaths have also a distinct pit in this place. The centra of the cervical vertebrae appears to be amphicoelous, as in Ichthyornis and Archaeopteryx, but additional preparation is needed before this can be finally determined. Some of these characters are important points of similarity with Archaeopteryx, Ichthyornis, the Paleogene paleognaths, and some of the Tinamiformes, whereas the similarities in certain details of coracoidal structure to modern Gruiformes, Strigiformes, and Coraciiformes are only superficial, as the Ambiortiformes are not closely related to any modern neognathous birds. The strong resemblance of Ambiortus to the Paleogene paleognaths in many characters suggests the possibility of possessing a paleognathous palate as well.

The third group of features is unique to the Ambiortiformes: acrocoracoid elongated with pointed tip; perpendicular position of procoracoid process; a long, flat and narrow scapular blade; the third clawed phalanx on the major digit of the wing (in modern birds there are usually two phalanges); dorso-ventral deepening of the vertebral centra. Most of these characters defining the Ambiortiformes are also likely to be archaic.

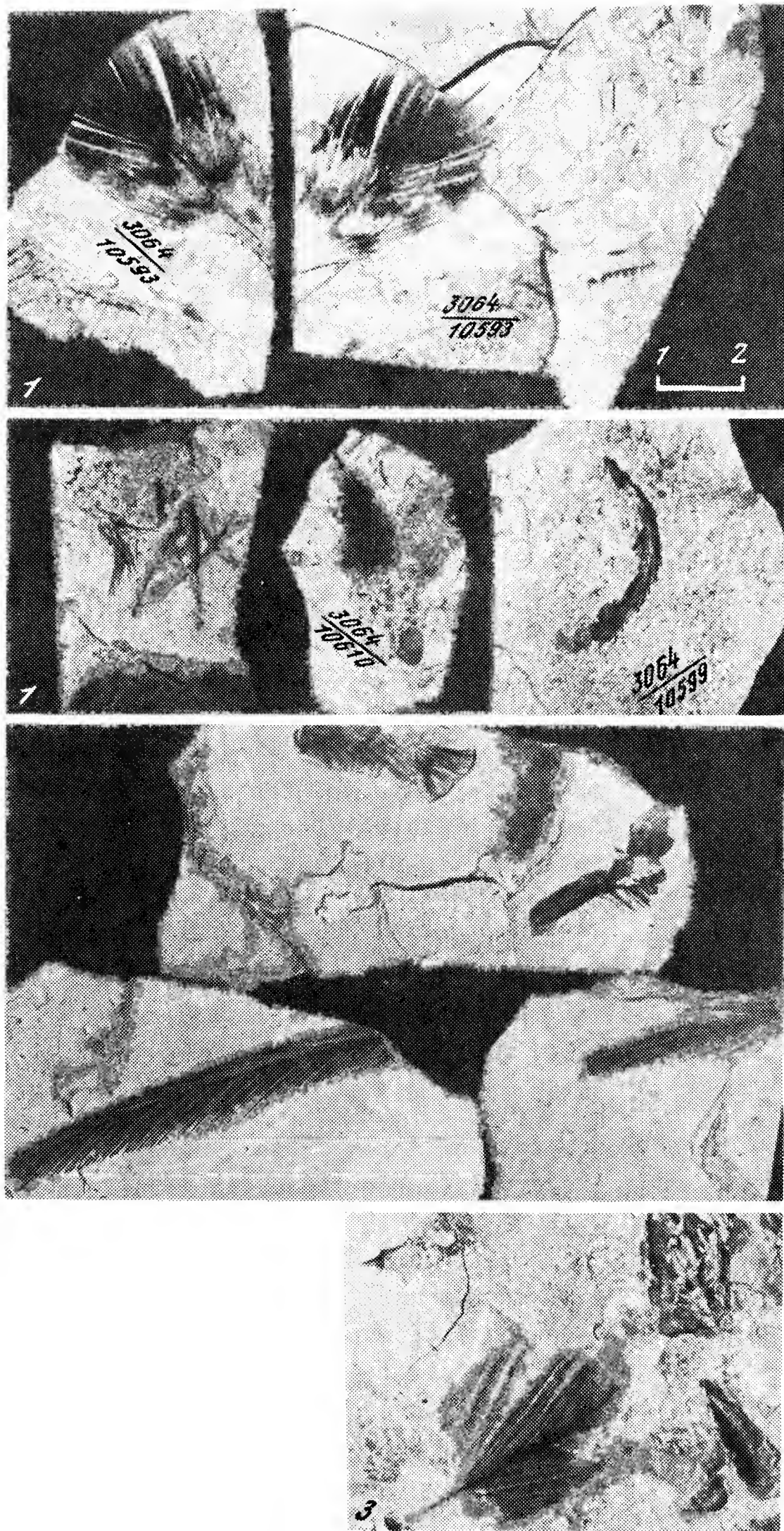
CONCLUSIONS

The Ambiortus is a true carinate, volante bird from the paleognathous group. At the same time this is the oldest carinate bird known in the world and oldest bird ever known from Asia. It appears to be basal to the Infra-class Carinatae and is characterized by a complicate mosaic of characters that are derived for **Aves** and archaic for carinates. The Ambiortus confirms

that mosaic of the skeletal structures formed by the heterochronias very likely was a common way in vertebrates evolution, probably in this respect birds distinguished a little from reptiles and mammals. At the same time heterochronias could lead out separate groups of birds on the different levels of morphological and ecological conditions. By this way some of them got an additional impulse for biological progress, but others dropped in deadlocks of evolution. If Ambiortiformes and Archaeopterygiformes being compared from these positions, it can be concluded that if there are phylogenetical relations between these orders, their relations are very ancient. The Ambiortus had a very long started over Archaeopteryx and there was no grounds for origin of Ambiortiformes from Archaeopterygiformes. At the geological times they are very close, one is from Lower Cretaceous, the other is from Uppermost Jurassic.

Ambiortus demonstrates now positively that advanced, volant carinate birds existed earlier in the Cretaceous. This point is confirmed by findings of numerous feathers impressions from many localities of Lower Cretaceous in Siberia, Mongolia and Australia, and bird footprints from the Aptian of British Columbia, Canada (Currie, 1981), that demonstrate a likely common and wide distribution of true birds at that time. So Ambiortus would have been close to the main line of avian evolution, but Archaeopteryx would have been a primitive relict on a side branch on the way from reptiles to birds. This position moves aside the origin of birds more deeply at the times, that it is commonly accepted nowadays. Such hypothesis is corroborated by other paleontological facts.

Not long ago from Middle Triassic of Spain a birdlike reptile Cosesaurus aviceps was described (Ellenberger and Villalta, 1974). Its morphology and evolutionary significance was considered in detail by P.E. Ellenberger (1977). Cosesaurus was found much close to birds, than to Archaeopteryx. There are especially many common resemblances in structures of the shoulder and pelvic girdles, as well, the skull, between Cosesaurus and birds. It has a feather-like patterns pointing out that this specimen was immature. It seems, that head's structures of long bones point out this too. P. Ellenberger considers that distinct bird branch appeared at evolution in Early Carboniferous. The archosaurian branch was going in parallel to the latter, and Archaeopteryx was a side and deadlock line in this branch. So, now we know one theropod dinosaur - Avimimus which had the consolidated distal parts of the forelimbs and hindlimbs (Kurzanov, 1981, 1982) and possibly was a feathered reptile. It confirms a possibility of a parallel way of the birds type extremities and feathers in the evolution. Then J. Jensen (1981) announced about the oldest bird Palaeopteryx from Jurassic of USA. The only certain Early Cretaceous bird is flightless Enaliornis from Albian deposits in England. Although no pectoral elements of Enaliornis are known, those of the Late Cretaceous Hesperornis and Baptornis show these genera to have been flightless (Martin, Tate, 1976) and Enaliornis may have been likewise. Enaliornis shows that by Early Cretaceous, highly specialized, possibly flightless diving birds had already evolved in subclass entirely different from Ambiortus. The considerable interest, in this respect is the recent collection of numerous imprints of Early Cretaceous feathers from five sites (from Hauterivian to Albian age)



F i g. 4. Feather impressions from some Lower Cretaceous localities of the USSR and Mongolia

1 - Bajsa site, USSR, Transbaikalia, age - Hauterive - Valanginien, slab of contour feather with colour pattern preserved; 2 - Gurvan-Eren site, Western Mongolia, age - Neokomian, primary, tail covert (?) and contour feathers; 3 - Shin-Huduk site, Central Mongolia, age - Neokomian, small contour feathers. Natural size

in Mongolia, including Hurilt-Ulan-Bulak locality of Ambiortus site, and Bajsa locality (Vallanginian - Hauterivian) in Transbaikalia, USSR (Fig.4). Most of them are small contour feathers but **others** can be discerned as primaries, tail coverts, and down feathers. Some of the Bajsa feathers even preserve **traces** of the color pattern. Unfortunately, even a large number of such feather impressions do not permit a determination of the **systematic** position of the birds from which they came. But their abundance indicates that birds were rather common in Early Cretaceous biotas and we may, thus, hope to find additional skeletal remains of birds of this age.

These new data demonstrate the distribution of parallel evolution between birds and their reptilian relatives and that real way of the birds origin was much more complicate than it is usually presented now.

ACKNOWLEDGMENTS

I am grateful to A.Ponomarenko, Ju.Popov, V.Zherichin and other paleontologists of the Paleontological Institute for discovering the holotype of Ambiortus and Early Cretaceous feathers imprints, so for the information on the ages of the localities discussed. S.Olson and R.V.Sleshinskaja generously assisted in the English translation. Details of the structure of the Paleogene paleognathous carinates were examined on the specimens placed at my disposal by P.Houde to whom I am greatly indebted for this courtesy and for discussing much unpublished information with me. For discussing the data on Ambiortus I am thankful to L.P.Tatarinov, S.Olson, W.Bock. For preparation of pictures I am indebted to A.Tarasenko.

This investigation was supported by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and by the Office of Fellowships and Grants of the Smithsonian Institution.

SUMMARY

A partial skeleton of a bird from Early Cretaceous deposits of Mongolia constitutes a new family and order (Ambiortidae, Ambiortiformes). The specimen of Ambiortus dementjevi Kurochkin, 1982 consists of the bones of the shoulder girdle and wing, a keeled sternum and vertebrae, as well as feather impressions. The skeleton presents a mosaic of archaic and specialized characters within the Class Aves and indicates that advanced carinate birds existed some 10-15 millions years after Archaeopteryx. The geological time and evolutionary level of Ambiortiformes support considerations that Archaeopteryx is not representative of a state of avian evolution in the late Jurassic. It is proved that Archaeopteryx and coelurosaurians were very close relatives, but most probably this branch of archosaurians developed in parallel to the branch of true birds. This hypothesis is more likely with discovering of Cosesaurus, Palaeopteryx and Avimimus from Mesozoic deposits of Spain, United States and Mongolia. The Ambiortus, together with numerous feather impressions from other early Cretaceous localities in Mongolia, Australia and Soviet Union, indicate that birds were probably common in early Cretaceous biotas.

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THE BIRDS OF WESTERN AUSTRALASIA

P.V.Rich, G.F.van Tets, C.Balouet

Earth Sciences Department, Monash University, Clayton, Victoria 3168,
and the National Museum of Victoria, Russell St., Melbourne, Victoria
3000, Australia; C.S.I.R.O. Wildlife Research, P.O. Box 84, Lyneham,
A.C.T. 2602, Australia; Institut de Paleontologie, Rue de Buffon,
Paris 5, France

INTRODUCTION

In comparison to the fossil records left by birds in Europe and North America, that of Australia is meagre (see Fig. 1-2). But perhaps this can be forgiven because of the poor exposure, and often deep chemical weathering of the sediments that could produce the goodies. Perhaps, too, one should realize that vegetation thickly covers many of those areas of topographic relief where long sequences of Mesozoic and Cainozoic rocks would be exposed were it not for the "trees". And then, too, vertebrate palaeontology as an active science is still youthful in Australia; the still too few workers have a lot of ground to cover, much of which is remote and not easily (either due to finances or terrain) reached.

Still, despite these harassments, there is something to be gained in looking at the fossil record, no matter how small, of birds during the past 130 million years (Fig. 3). At present it (1) offers insight into short term (for the past 15 or 20 million years) evolutionary patterns within Australian birds, (2) records birds not known in the modern avifauna of this continent, (3) allows speculation on biogeographic and palaeoclimatic adjustments from the Miocene to recent, and (4) perhaps offers some insights (mostly in the form of a note of caution) into the origins of Australian birds.

THE FOSSIL RECORD OF BIRDS IN AUSTRALIA

Geographic and Stratigraphic Distribution

Unfortunately the fossil record of birds in Australia is not the excellent one of Europe and North America, and in fact it is essentially one restricted to the Neogene and Quaternary (Rich, 1975a,b; Keast, 1981). The best record in Australia, like elsewhere in the world, occurs during the Quaternary where the numerous cave deposits in eastern and southern Australia add large samples to an all too depauperate record. The longest, although discontinuous, record of birds occurs in central Australia in the Great Artesian Basin (Lake Eyre and Lake Tarkarooloo Subbasins), and this record spans the Miocene to the recent. Although dinosaur bone has been recorded in Mesozoic sediments in the same area, no birds have been recovered from the older sediments. The majority of avian fossil sites, when the entire record is considered, are from the eastern half of Australia. Only a few Pleistocene sites are known in the western half, and so far little can be said about the biogeography of fossil birds on the Australian continent through the late Mesozoic and Cenozoic.

Although some of the oldest remains of birds in the world occur in Australia, the early Cretaceous feathers (see Fig. 4) of Koonwarra, there is a large

Fig. 1. Number of localities per Epoch/Era producing fossil birds with geographic subdivisions: A - Australia; AF - Africa; AS - Asia; EU - Europe; IS - Island; NA - North America; SA - South America

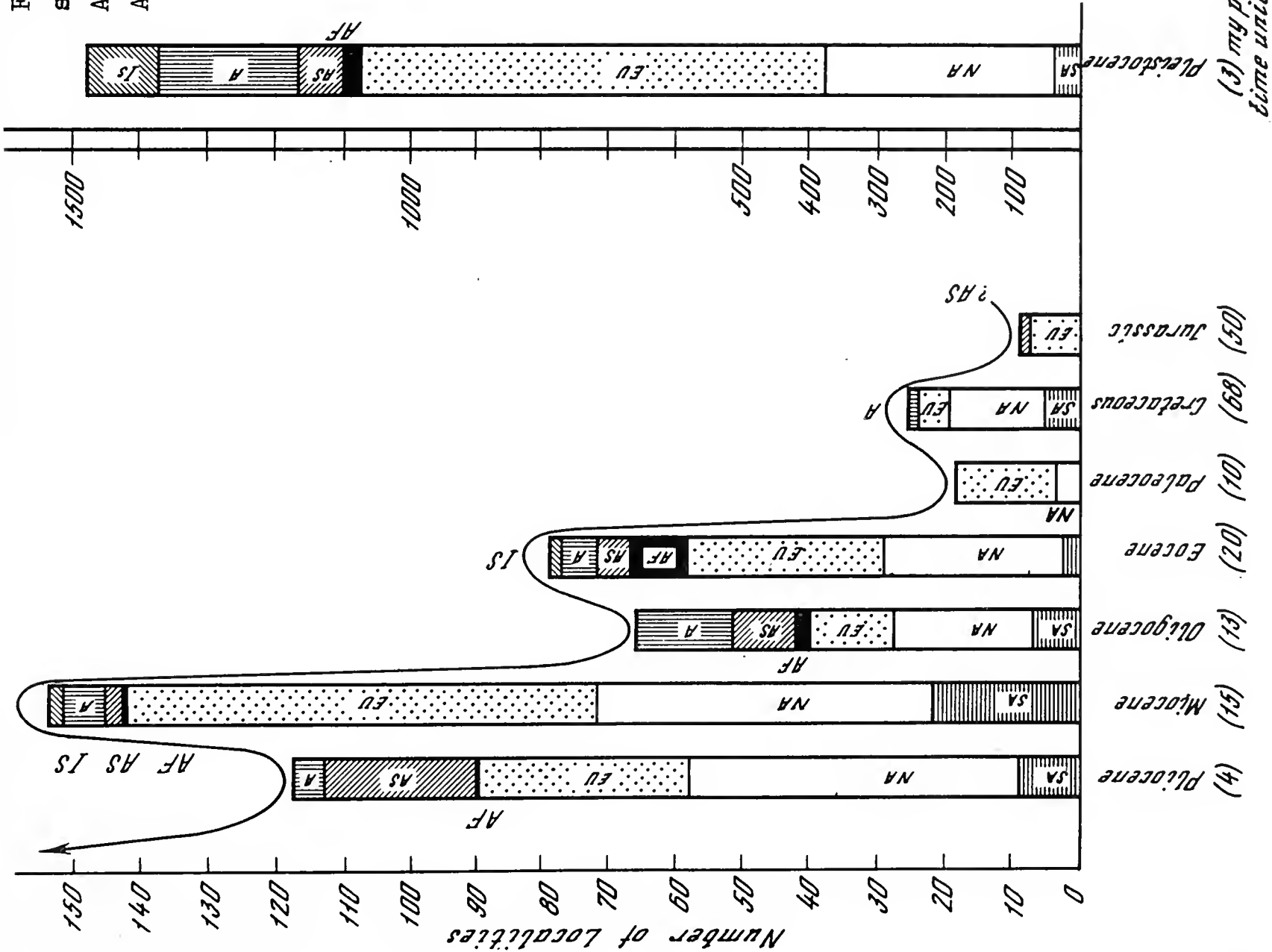
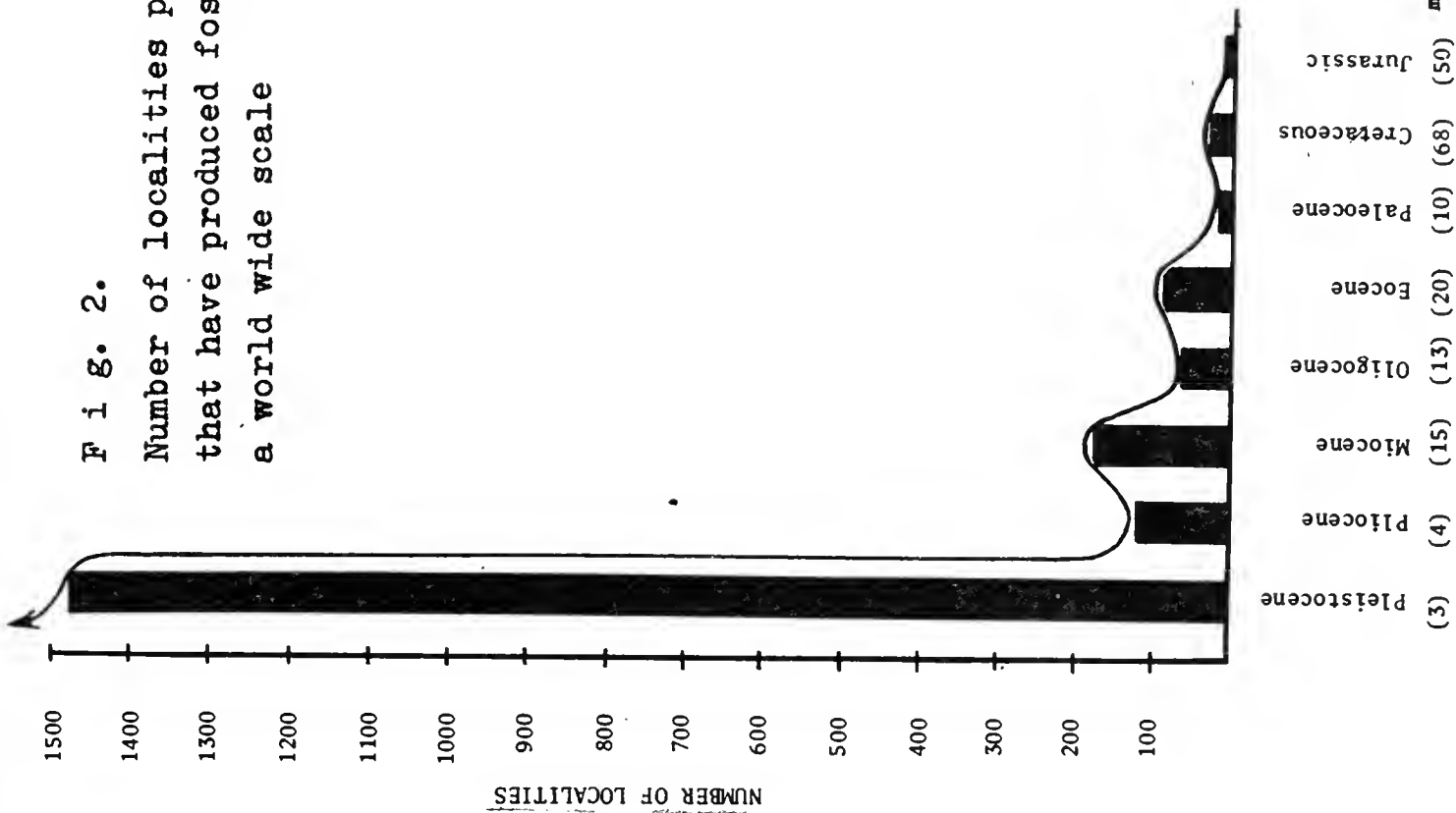


Fig. 2.

Number of localities per Epoch/Era that have produced fossil birds on a world wide scale



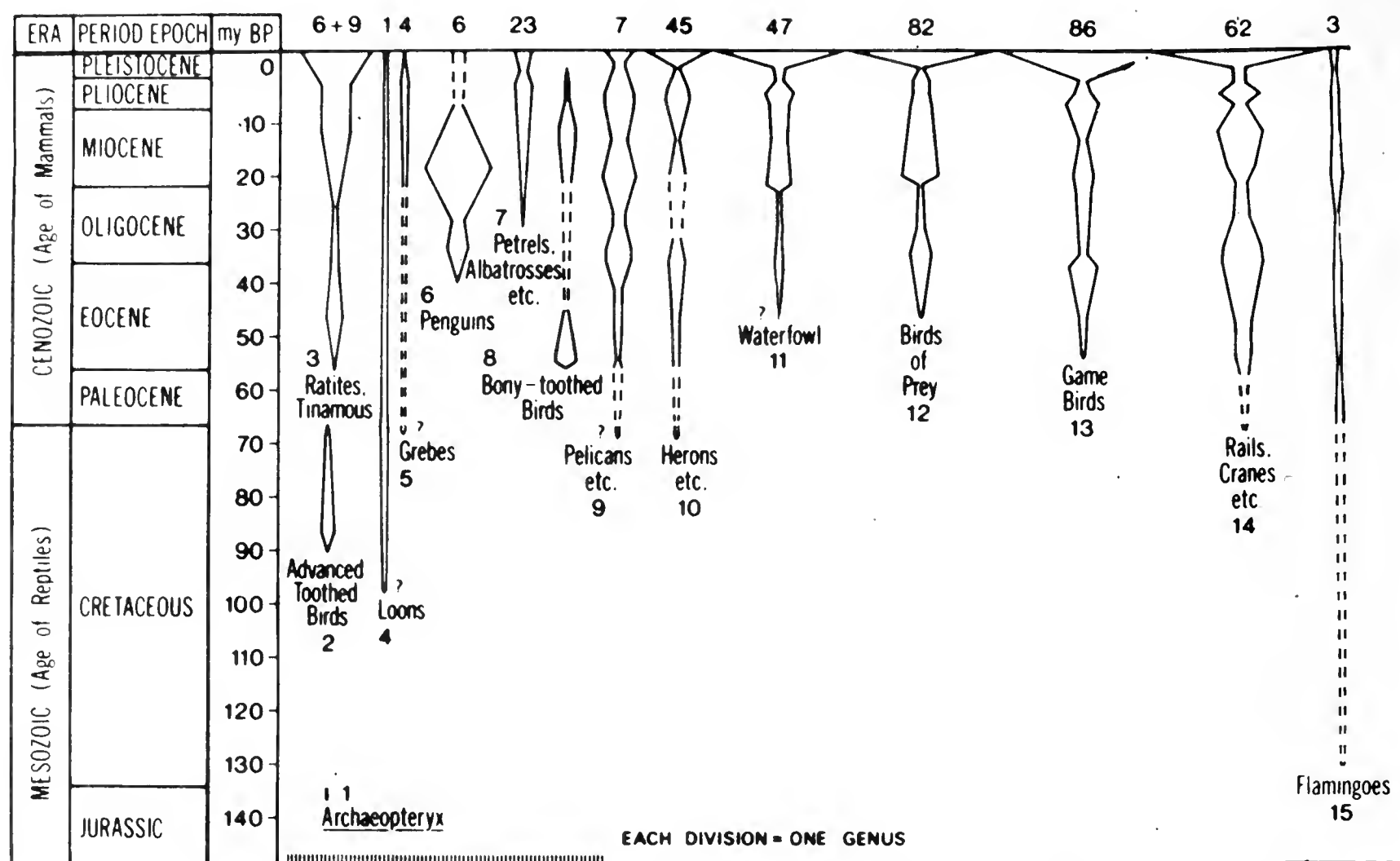


Fig. 3. Generic diversity of avian orders in pre-Holocene deposits. Width of columns indicates number of genera (see scale at bottom left). Numbers in the main body of chart contain the groups enumerated in Table 1



Fig. 4. A variety of feathers recovered from Early Cretaceous lake sediments in the Strezlecki Group of Gippsland; southern Victoria. All are small, averaging about 20 mm in length

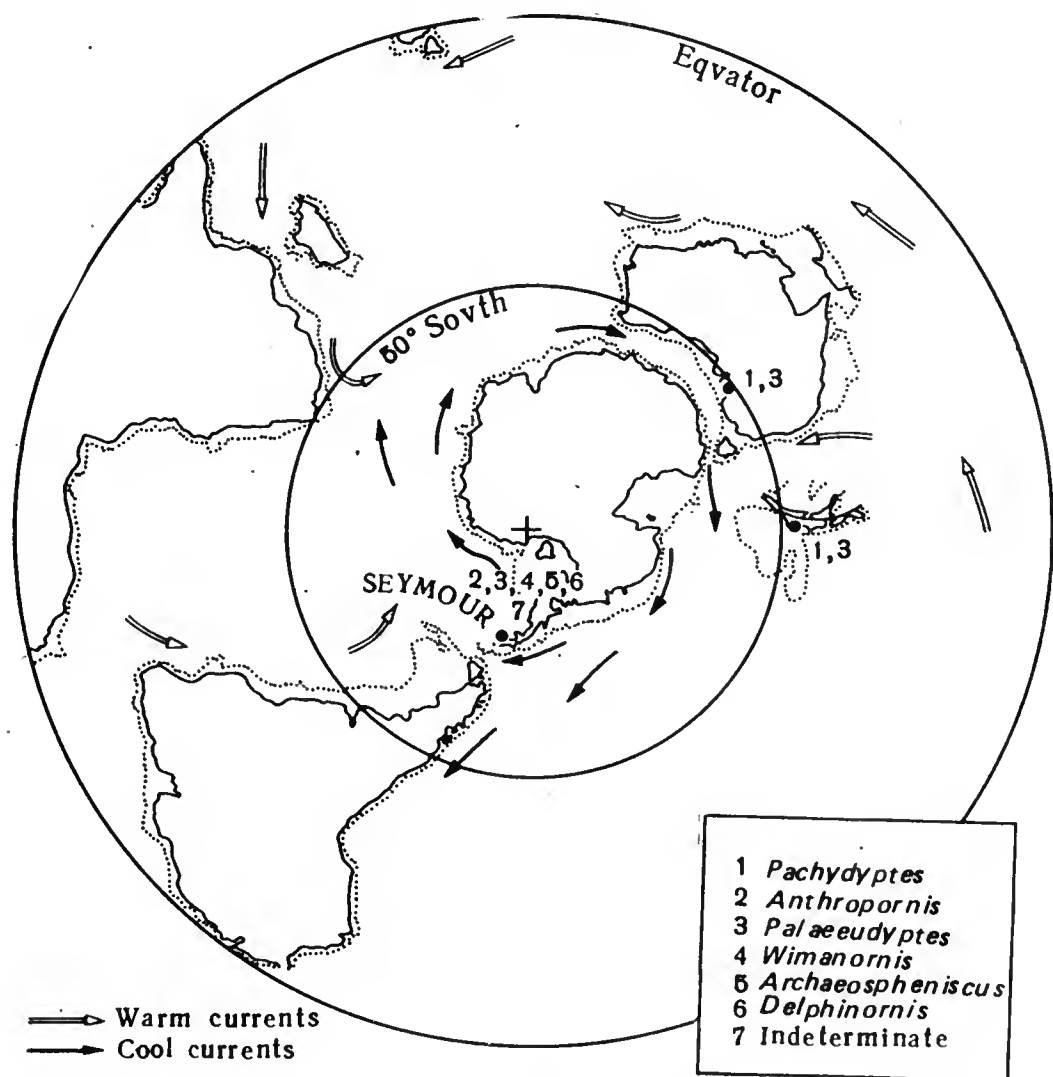
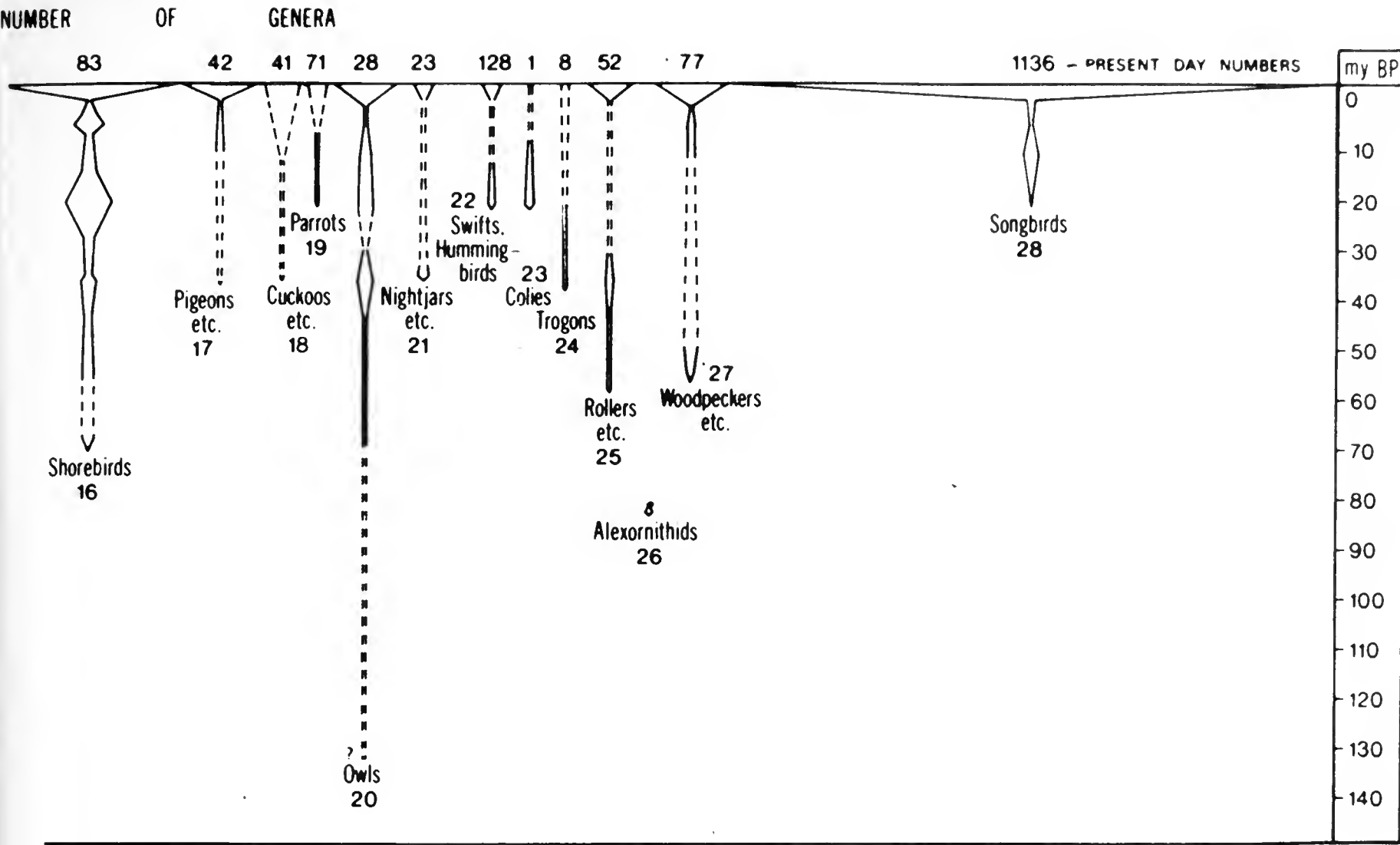


Fig. 5. Late Eocene fossil penguin localities plotted on a palaeogeographic map for this time period. Arrows indicate hypothetical pattern of oceanic surface circulation (after Jenkins, 1974)

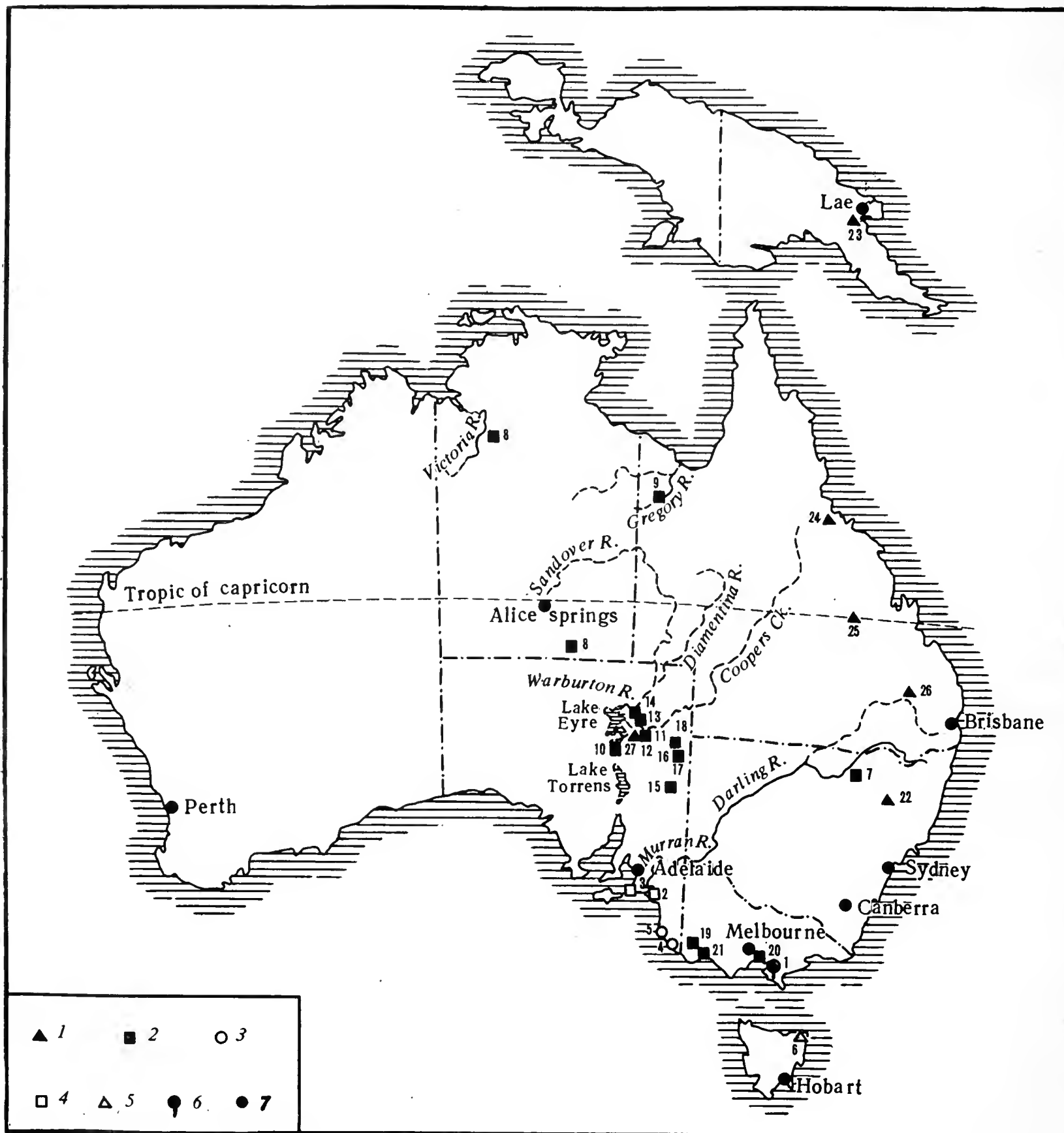
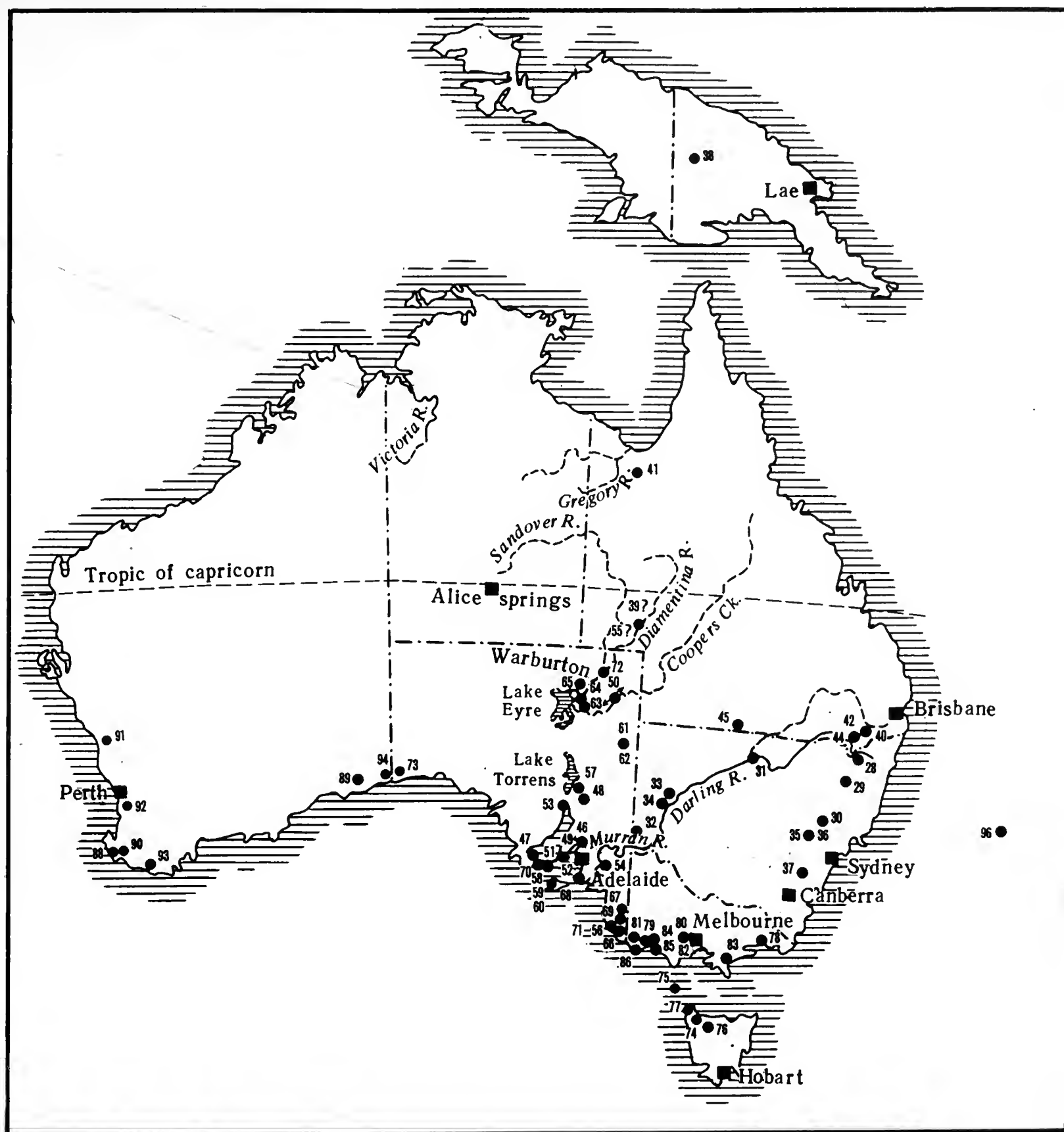


Fig. 6. Fossil bird localities of Australia

1 - Pliocene; 2 - Miocene; 3 - Oligocene; 4 - Eocene; 5 - Mid-Tertiary;
6 - Cretaceous; 7 - Pleistocene

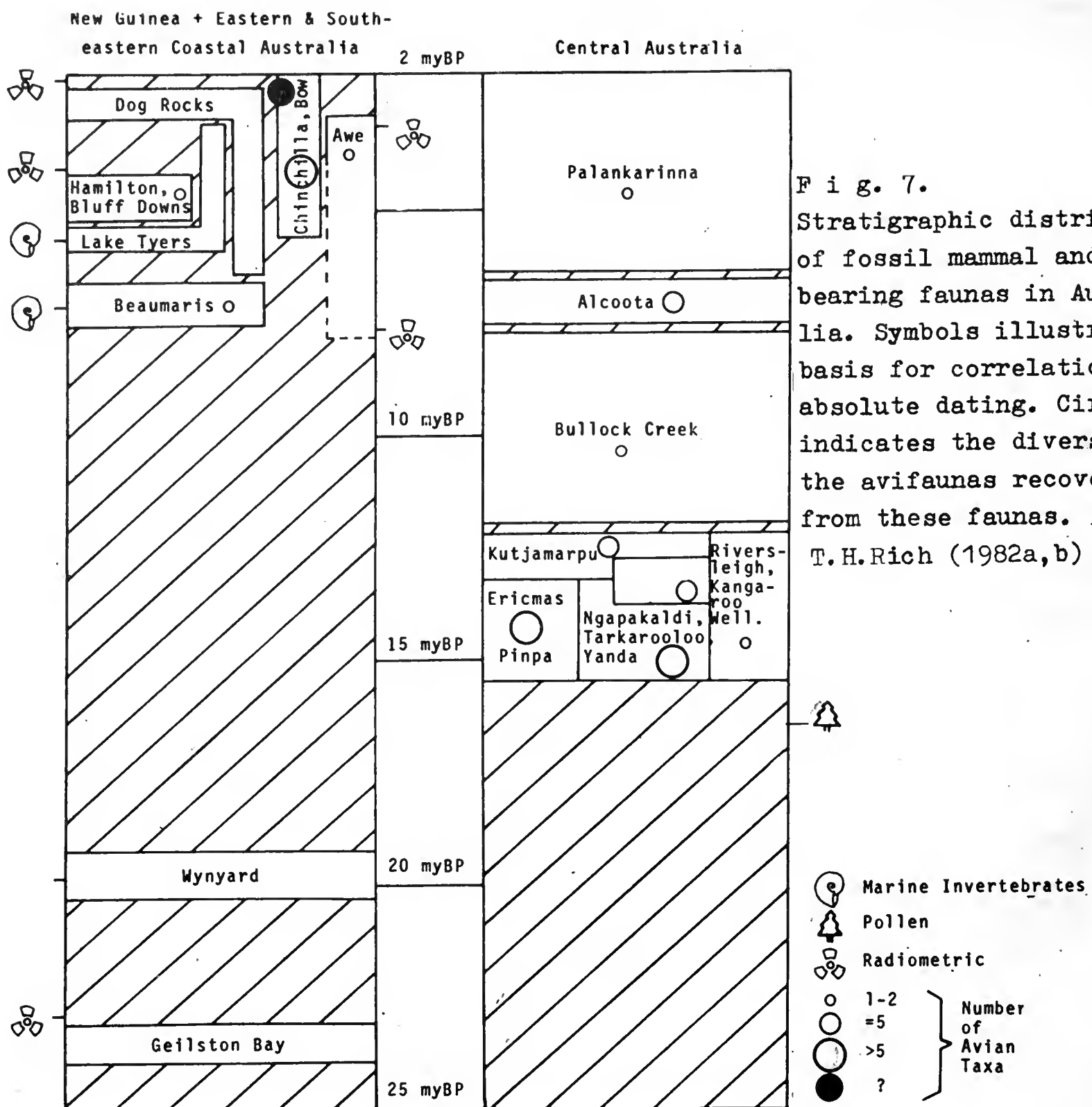
time gap between these feathers and the first occurrence of a variety of species of birds. The Koonwarra feathers are of several types and most have tertiary branching preserved, but thus far they have defied identification beyond Aves Indeterminate. Further studies underway (Duncan and Rich) may shed further light on their identity.

Paleogene records are those of penguins (see Rich, 1975a, b; 1976), from localities in the southeast of Australia (South Australia) and are forms thought closely related to the genus Palaeudyptes also known as fossils in New Zealand and Seymour Island (W. Antarctica), but more diverse than modern



genera of penguins. Another very large penguin Pachydyptes simpsoni, also from southeastern Australia (near Adelaide) has been recovered from Late Eocene sediments and represents a bird markedly larger than any living penguin. The genus Pachydyptes is also known from Late Eocene and Early Oligocene sediments in New Zealand, and both are similar to another form, Anthropornis, which is reported only from Seymour Island. Simpson (1971a,b) pointed out that Palaeodyptes - Pachydyptes - Anthropornis were all closely related genera, and in fact they may have descended from a common stock. Figure 5 shows the distribution of Eocene penguins, land masses and water currents that suggest why the penguins of Antarctica, Australia, and New Zealand were similar (from Jenkins, 1975).

Only in the Neogene do the fossil avifaunas contain more than an occasional bone, and the earliest faunas are best preserved in central Australia in the Great Artesian Basin, especially at Lake Palankarinna in South Australia, (see earlier summaries in Rich, 1975a,b; 1976, 1981). The dating on these rock



sequences is not based on the birds but on pollen data, to some extent, and on the diprotodont marsupials. No absolute dates are possible because of the lack of igneous rocks in the region. The pollen used that is then correlated to sections further south (which contain both pollen and foraminifera allowing further correlation to European type sequences), most often occurs in drill cores not adjacent to the vertebrate fossil localities, although at least one at Mammalon Hill, Etadunna Formation, Lake Palankarinna (Pledge, 1982) (see Fig. 6) had produced pollen associated with vertebrate fossils and another (at Leaf Locality, Wipijiri Formation, Lake Ngapakaldi, South Australia) has produced macroplant remains. Thus, correlations, for the most part based on pollen have been from vertebrate fossil locality by lithologic similarity to well cores nearby bearing similar sediments containing pollen, thence from there to sections or cores bearing pollen and foraminifera, thence from Australian foram bearing sequences (often via many steps!) to the foram bearing European sequences. In practice correlation has been based too on the "stage of evolution" of the marsupial fossils compared to those of other localities such as Beaumaris. Victoria (which has marine fauna of Cheltenhamian

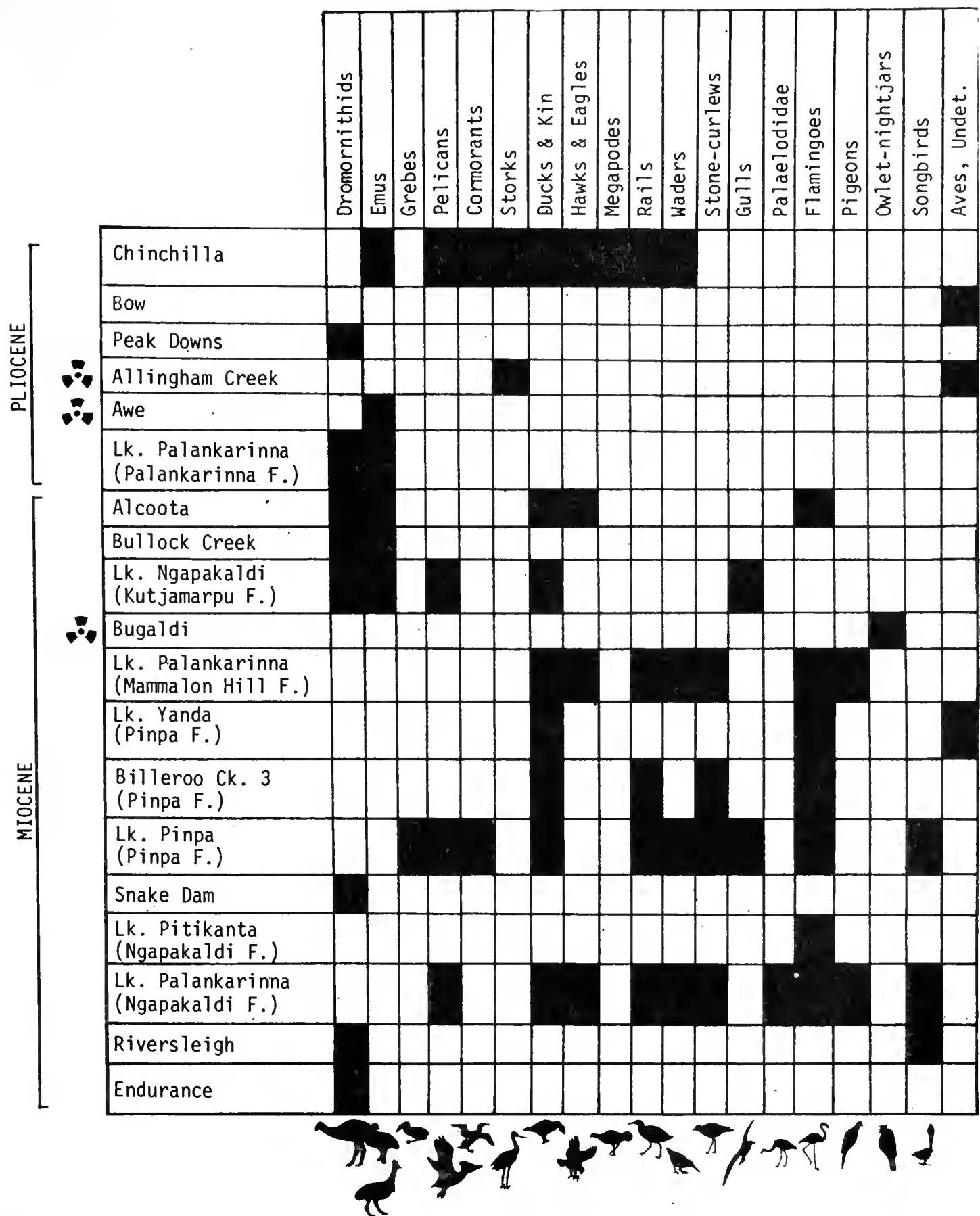
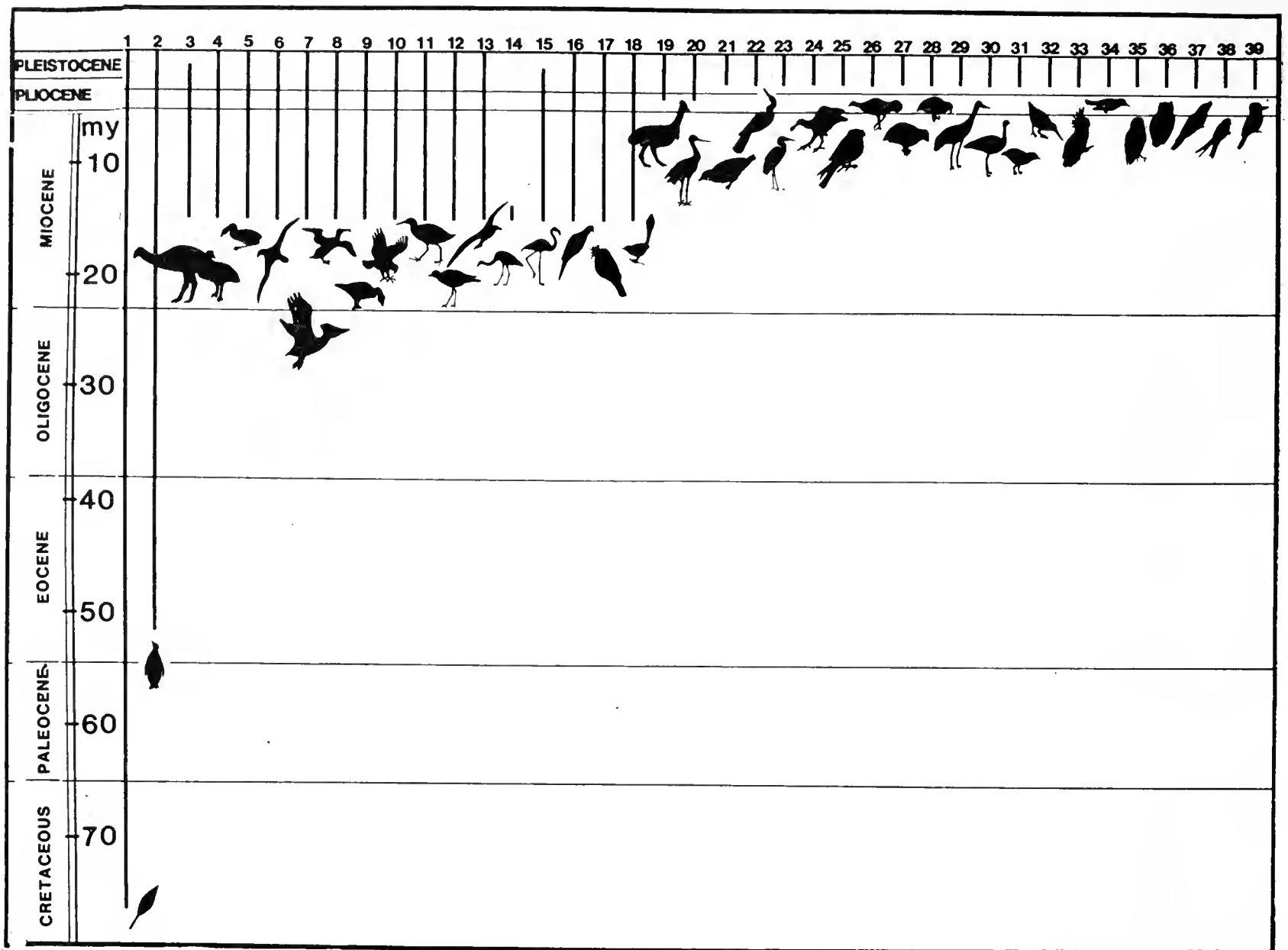


Fig. 8. Record of different avian families in the Australian Neogene. Indicates localities with radiometric or invertebrate (marine) dates. F = fauna. Faunas roughly in stratigraphic order, but some, such as the Ngapakaldi Fauna and the Pinpa Fauna may be contemporaries

or late Miocene age associated with terrestrial diprotodont marsupials, such as *Zygomaturus gilli*) or Hamilton, Victoria, (which is overlain by a basalt dated at 4.35 million years and underlain by a Kalimnan aged or early Pliocene marine fauna and which contains a number of fossil marsupials) where absolute dates can be assigned. Vertebrate bearing sites with absolute dates in Australia, however, are all too rare (Stirton, Tedford and Woodburne, 1968; Rich T.H. et al., 1982).

Despite the problems with correlation, the "Neogene" avifaunas can at least be put in superpositional arrangement, as at Lake Palankarinna in the



F i g. 9. Geologic ranges of Australian birds

Lake Eyre Subbasin (Great Artesian Basin, Loc. 9, Fig. 6) and at Lake Pinpa in the Tarkarooloo Subbasin (Loc. 10, Fig. 6), superposition of such faunas as the Ngapakaldi, Mammalon Hill, and Palankarinna in the first case and the Ericmas and Pinpa faunas in the second can be demonstrated (Fig. 7).

Composition and Bias of the Australian Neogene Avifaunas

The Ngapakaldi Fauna recorded from a number of localities in northern South Australia (best represented at Lake Palankarinna) contains the first diverse avifauna (see Figs. 8-9) from Australia, which consists of pelicans (Pelecanidae), flamingoes (Phoenicopteridae) the flamingo-like Palaelodidae (previously recorded only from Europe and North America), ducks and kin (Anatidae), hawks and eagles (Accipitridae), rails (Rallidae), waders (Charadriiformes) including abundant Burhinidae (thick-knees or stone curlews), pigeons (Columbidae), and songbirds (Passeriformes). A fauna that is probably contemporaneous, and not far separated geographically, the Pinpa Fauna, adds grebes (Podicipedidae), cormorants (Phalacrocoracidae), and gulls (Laridae) to this list. The most diverse groups in these early faunas are the Anatidae and Phoenicopteridae. Based on such early Neogene faunas some generalizations can be made about (1) faunal composition; (2) "stage of evolution" of the birds; (3) controls on what types of birds are represented and wheather these faunas are biased.

As with most of the Neogene avian assemblages known on a world-wide scale, the fauna consists primarily of wetland birds. Only such groups as mihirungs

(Dromornithidae), emus (Dromaiinae), birds of prey (Falconiformes) pigeons (Columbidae), and owlet-nightjars (Aegothelidae) are not strictly tied to lacustrine or fluviatile environments. Ducks and flamingoes and their kin certainly are, and are by far the most diverse in the preserved assemblages. This most likely is a preservation bias, as most of the productive sediments are those left by lakes and streams (see below), and that factor increases the likelihood of birds living in those environments being preserved.

The flavour of the Neogene faunas (or "stage of evolution" of its various members) is that it is a mixture of modern and archaic taxa. For the most part modern families are represented (such as Pelecanidae, Anatidae, etc.), but included are such archaic elements as the flamingo-like Palaeolodidae and the dromornithids, large to gigantic ground birds that were very diverse at the beginning of the Australian avian record and dwindled to extinction in the Pleistocene. The archaic elements probably represent the end members of a Palaeogene radiation that we have only a glimpse of by the Miocene. In these early Neogene faunas, too, there are families like the flamingoes that survive outside of Australia today but have no living members on this continent.

Within the modern families represented in early Neogene sites, the genera are often relatively primitive. Quipollornis, an owlet-nightjar (Aegothelidae) recovered from lacustrine sediments overlain by a basalt ranging in age from 13.5 to 17 million years, clearly belongs within the family of owlet-nightjars. Its wings are much longer relative to its hind limbs, and the hind limbs are not elongated, suggesting that it was an aerial insectivore, more like the Caprimulgidae (nightjars) than like the more terrestrial feeding owlet-nightjars. Some members of the Caprimulgidae may have given rise to the Aegothelidae. Based on the evolutionary patterns seen in Miocene birds of the rest of the world, this is exactly what would be expected in a typical mid-Tertiary mosaic bird. Emus found in early Neogene sediments also are more cassowary-like in that the medial digits are not as reduced and the distal hind limb elements not as elongate as in the more cursorially adapted living Emu (Dromaius novaehollandiae). By the end of the Neogene (and for some groups such as the pelicans and emus) modern genera have appeared, and certainly during the Pleistocene many modern species appear. In fact, many of the Pleistocene species that originally had been coined as presently extinct (De Vis, 1885, 1888 a-b, 1889, 1890, 1891 a-c, 1928, 1905, 1911) have since been found to be indistinguishable from living species. Because De Vis (who worked at the Queensland Museum for several years) had a relatively poor comparative collection and the attitude that fossils must represent extinct species, a great number of new species were erected for Pleistocene fossils. In cases where modern species extend into the Pleistocene occasionally the range during that period is decidedly different than it is today (for instance, the Tasmanian Native Hen (Tribonyx mortierii) in Queensland (Olson, 1975) and elsewhere in southern Australia.

Although the above conclusions have been drawn about the Neogene avifaunas of Australia, interpretations must be tempered by the knowledge that every one of these assemblages is highly biased; (1) few specimens are complete; (2) most often certain skeletal elements are abundant while others are lacking or rare; (3) most bird fossils are of medium-size, and very few are small.

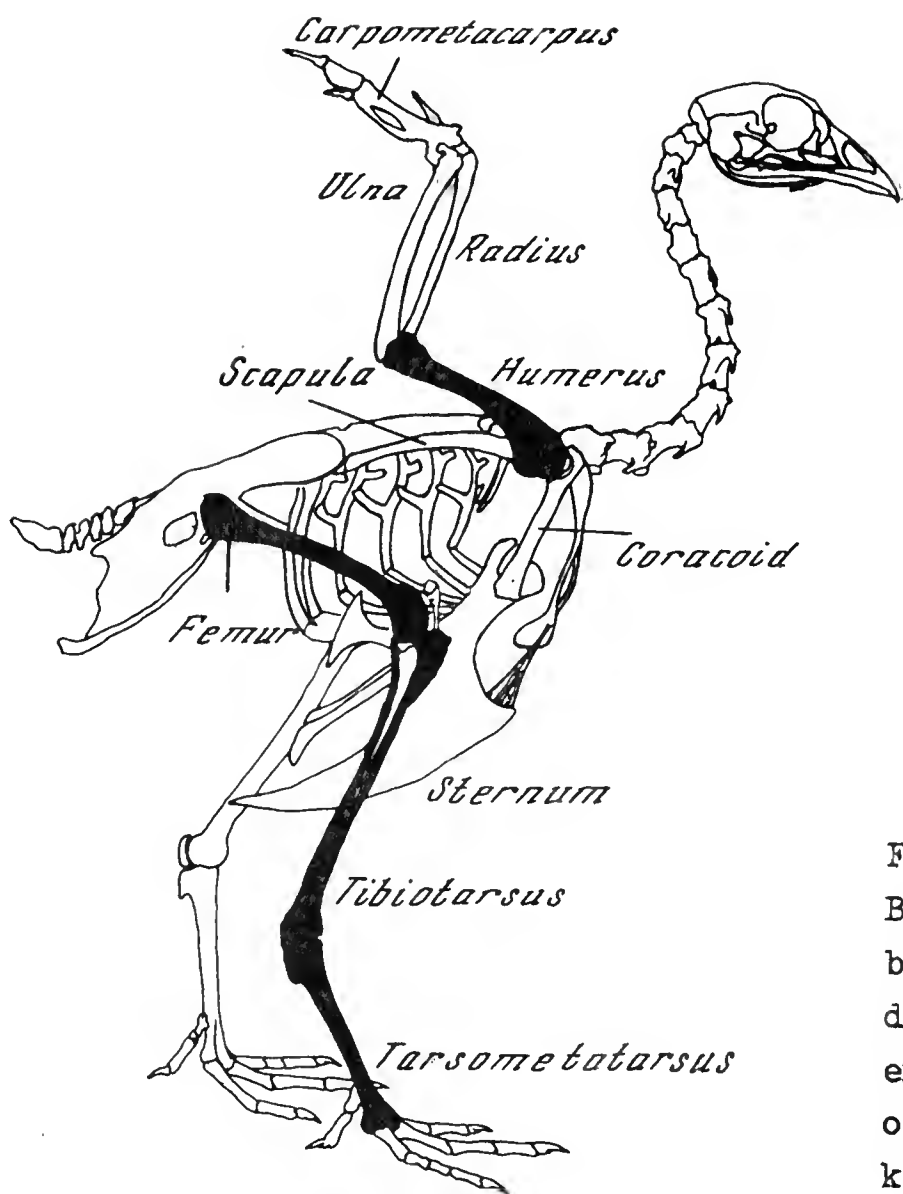


Fig. 10.

Bird skeleton illustrating those bones (black) most resistant to destruction in simulated fluvial environments (tumbler experiments of Napawongse, 1981), thus most likely to be fossilized

All of these factors point to biasing that occurs in fluvial sediments as discussed by Wolff (1973, 1975). And, in fact, most localities that have produced avian fossil assemblages are fluvial in origin; a few are lacustrine, such as the Bugaldi site that produced *Quipollornis*, a rare nearly complete skeleton with feathers preserved. A few of the localities at Lake Palankarina are lacustrine, and one (Neville's Nirvana) has produced partially articulated material of the flamingo-like palaelodids. Fewer sites still are marine in origin, and these have produced mainly disarticulated penguin material, of ten terribly worn, and fragments of albatross (e.g. *Beaumaris* in Victoria).

In the fluvial sites, as noted above, certain elements are more abundant than others, and bones are often not complete. For example, humeri, coracoids, tibiotarsi, and tarsometatarsi are most frequently represented, and often the distal ends of the tarsometatarsus and the tibiotarsus as well as the distal end of the humerus are most frequent (Fig. 10). Observations at other fluvial-derived sites (Rich, 1980a) as well as simulated fluvial systems (Napawongse, 1981) suggest that these bones are the most resistant in a bird's skeleton to erosion. In the same sites, birds of medium to large size are preferentially selected for. Small birds are underrepresented and found only in a few of the sites; when found they are often rare within the site, i.e. two passeriform bones have been found at Riversleigh even though this site is credited with small birds. This is repeated at many other sites listed as having produced small fauna. There is no single locality in Australia in the pre-Pleistocene that has produced a diverse avian microfauna, despite the fact that many sites have been extensively screen washed (McKen-

na', 1962). The action of the fluviatile environment on the avian bones prior to burial has presumably brought about many of the above biases, and thus in any interpretation of the fossil avifaunas, such biasing must be borne in mind. Some sites, in fact, such as the Pliocene Hamilton locality in Western Victoria and the Miocene-aged Tommo's Quarry at Lake Tarkarooloo, S.A., even though they have produced dental remains of mammals, have never produced bird bones. These sites evidently represent thanatocoenoses ("death assemblages") that have travelled a long, "eroding" distance from the places individual animals died, and presumably the fragile bird bones have been lost. When, for instance, the observation is made that parrots are only known from Pleistocene or younger sediments in Australia, yet they are extremely diverse in Australia's modern avifauna, their lack of occurrence in older sediments may well be preservation bias, and not necessarily a reflection of their real record on the Australian continent.

Phylogenetic Lineages and Biostratigraphic Usefulness of Birds in the Cainozoic Australian Record

Of the fossil birds that are known in Australia today, only a few groups have both a good representation and have been studied sufficiently so that a reconstruction of phylogenetic lineages can be attempted: The Dromornithidae, Casuariidae, Pelecanidae, Phoenicopteridae, and Aegothelidae. As reviews of some groups progress, the Phalacrocoracidae, Anatidae, and Rallidae will offer an equal possibility of phylogeny construction and biostratigraphic utility. The Palaeolodidae may prove useful in inter-continental correlation between Australia and Holarctica.

The main problems in construction of such lineages have been, in part, mentioned above: the material is often fragmentary and quite incomplete; often taxa being compared are not represented by comparable elements; there are many hiatuses in the rock sequences from site to site, and thus more or less continuous sequences where gradual or punctuate changes might be observable are non-existent.

Despite these problems there are some intriguing absences of groups in certain areas that may be significant, some of which can be explained. For instance, emus are absent in the oldest fossiliferous sediments in both the Lake Eyre and Tarkarooloo Subbasins. Perhaps this is a preservation bias against big birds, but one begins to suspect because the sample size is relatively large, and because marsupials of emu-size are present, that perhaps the reason emus are not present is that they really were absent and that the area was sufficiently forested not to be attractive to emus. Flamingoes are present only in central Australia and were evidently tied to shallow, permanent alkaline lake environments much like those of East Africa today. Once those permanent environments disappeared sometime in the Pleistocene, the flamingoes became extinct. Other birds such as the Pink-Eared Duck (Malacorhynchus membranaceus), seem to have coped with the disappearance of permanent shallow lakes by utilizing alternative sites in times of drought, and moving back into the interior lakes in times of wet conditions. Flamingoes, whose reproductive cycle depended on the constant presence of these lakes, failed to survive. Another bird that survived that uses the salt lakes for breeding, the Banded Stilt (Cladorhynchus leucocephalus), is able to delay breeding until

the salt lakes are filled. Both birds appear to be more adaptable than the Australian flamingoes.

The representation of two other groups, the parrots (Psittaciformes) and the ducks, can probably be explained by preservation bias. Parrots are extremely diverse, both at lower and higher taxonomic levels in Australia today, which hints at a long history of this group on the Australian continent (or an explosive radiation in Australia in the mid to late Cainozoic). Because these parrots are not waterbirds, their chances of preservation are slight and in fact, their record on a world-wide scale is poor (Brodkorb, 1971). Ducks, on the other hand, are very diverse, which is also probably due to their nearly constant association with water, thus having a greater likelihood of being incorporated into a lacustrine or fluviatile sediment.

In order to convey what information is available on avian groups, emphasis on those of biostratigraphic usefulness, a brief resume of the fossil record of those avian families with a reasonable record in Australia follows (Rich and van Tets and Fordyce in Rich and Thompson, 1982, have summarized much of eastern Australasia).

Casuariidae - Emus and Cassowaries

This group first appears in the late Miocene and continues to the present day. Patterson, 1980, has described the oldest species in this genus from the Miocene Wipijiri Fauna of Lake Ngapakaldi. Dromaius ocypus (Miller, 1963a), the next younger species that has been named, was found in Pliocene sediments at Lake Palankarinna (Lawson - Daily Quarry). In the Pleistocene D. novaehollandiae appears, but on the mainland the size range is greater than seen in present day members of this species, with very large forms present at times during this period. Three separate, smaller species may have developed on King Island, Kangaroo Island, and Tasmania that are currently under review by Shane Parker (So. Aust. Museum). These species overlapped with Europeans and were quickly wiped out by European settlement. In Pleistocene sediments, emu eggshell is a frequent component.

Trends observed through time within the Dromainae are (1) specialization of the proximal end of the tarsometatarsus; (2) decrease in size of digits II and IV; a 10% decrease in linear measurements is observed from Miocene-Recent in digit II, while a 3% is characteristic for IV; (3) the phalanges are compressed dorsoventrally; (4) the tibiotarsus and tarsometatarsus become relatively more elongate; and (5) there is an overall increase in size.

Cassowaries, the more primitive, less cursorially adapted members of the Casuariidae are known from Pliocene sediments (The Awe Fauna) in New Guinea, but only from two bones, which have been called Casuarus sp. (Plane, 1967). Another undescribed collection of cassowary bones is known from the Pleistocene of Purini, New Guinea; several skeletal elements are present. The only fossil species is Casuarus lydekkeri, which may be conspecific with C. bennettii, a small New Guinea species that also occurs on New Britain. The holotype and only known material of C. lydekkeri was supposed to come from a cave in the Wellington Valley of New South Wales, but its state of preservation and colour of the adhering matrix is unlike that of bones found in the Wellington area, or for that matter caves of eastern and southern Australia. The bone looks similar in preservation to those which have been recovered from

the Darling Downs of southeastern Queensland, also in part of Pleistocene age.

With the above information a rough estimate of biostratigraphic position could be made on the basis of certain bones of emus, but not cassowaries at present.

Dromornithidae - Mihirungs

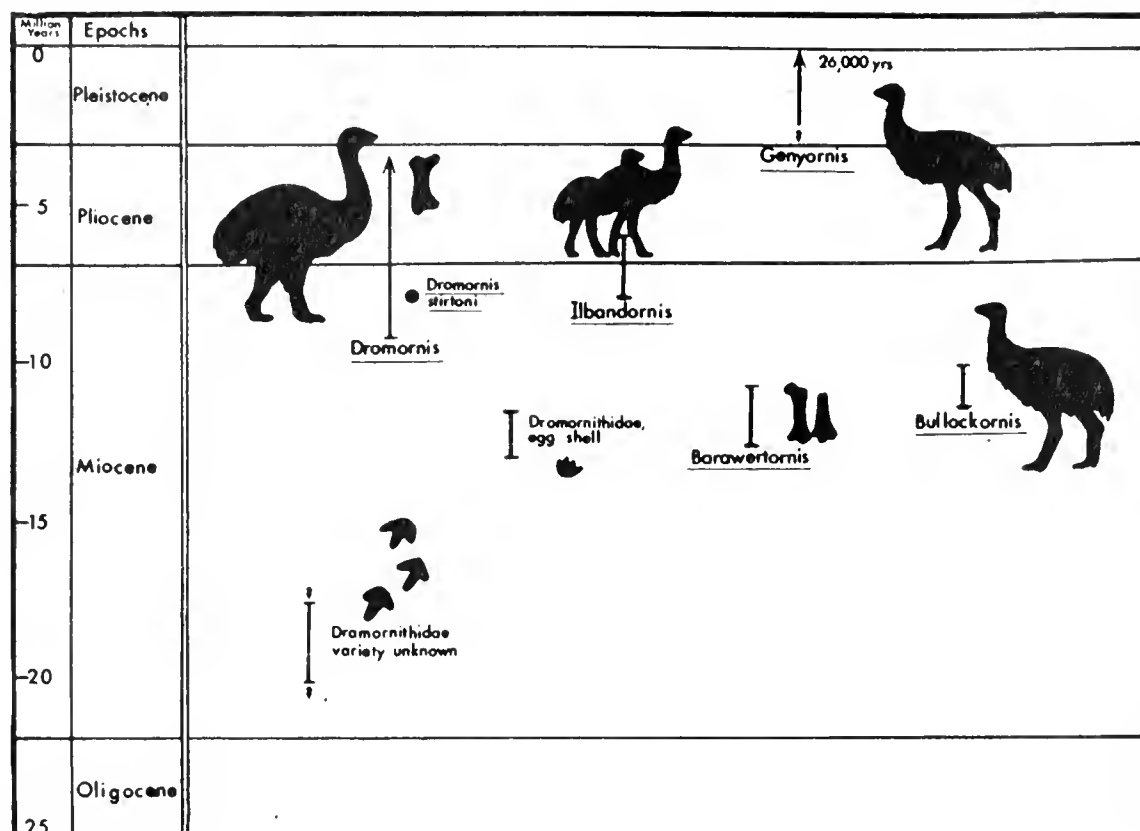
The most abundant and best documented group of fossil birds in Australia are the dromornithids - they are the diprotodontids of the bird world: The most recent work is contained in Rich and Green, 1974; Rich, 1975a, b, 1976, 1979a, b, c, 1980b, 1981; Rich, Gill, 1976; Williams, 1980, 1981). Broad biostratigraphic pronouncements can be made utilizing this group, but a refined set of divisions is not yet possible.

Dromornithids are representatives of an order or family of presently extinct birds that are endemic to Australia. They were large and flightless (see Fig. 11-14) with unique, hoof-like ungual phalanges. They ranged in size from about the size of, or slightly smaller than, emus to the largest birds known to have existed (Guinness Book of Records, 1981), probably larger than the Aepyornithidae, the elephants birds of Madagascar. Best known is Genyornis newtoni, from the southeastern quadrant of Australia that may have been the "mihirung paringmal" of aboriginal legends (Rich, 1979b, 1981). The group survived until at least 26,000 years ago (Gillespie et al., 1978). Although often referred to as "giant emus", the dromornithids are quite distinct from the Casuariidae, especially in the structure of the quadrate (Rich, 1982) and may in fact not even be ratite birds. The group is not well represented by cranial material, i.e. the palate is unknown, but the quadrate is unique, and the lower jaw, unlike that of others ratites is heavy and deep.

Dromornithids are known primarily from bony remains but also have left tracks in mid-Tertiary (Rich, Green, 1974) and Pleistocene rocks (Rich, Gill, 1976) and eggshell (Williams, 1981; Williams, Rich, 1982), and gastroliths (Williams, 1981; Rich, 1979b; Stirling, Zietz, 1900) in Neogene-Pleistocene sediments. Although not entirely conclusive, the tracks seem distinguishable from those of contemporary emus in the mid-Tertiary (Rich, Green, 1974) and the egg-shell is distinct from emu.

The shell of Genyornis has a smooth surface with a mean thickness slightly greater than Emu (D. novaehollandiae) shell, and the surface is marked by short, sub-parallel grooves, each associated with a single shell pore. The shell resembles the innermost layer of the Emu shells, but is 30% thicker and there is no indication that another layer existed (Williams, 1981). Such eggs were approximately 125 mm wide, 155 mm in length, and weighed about 1.3 kg.

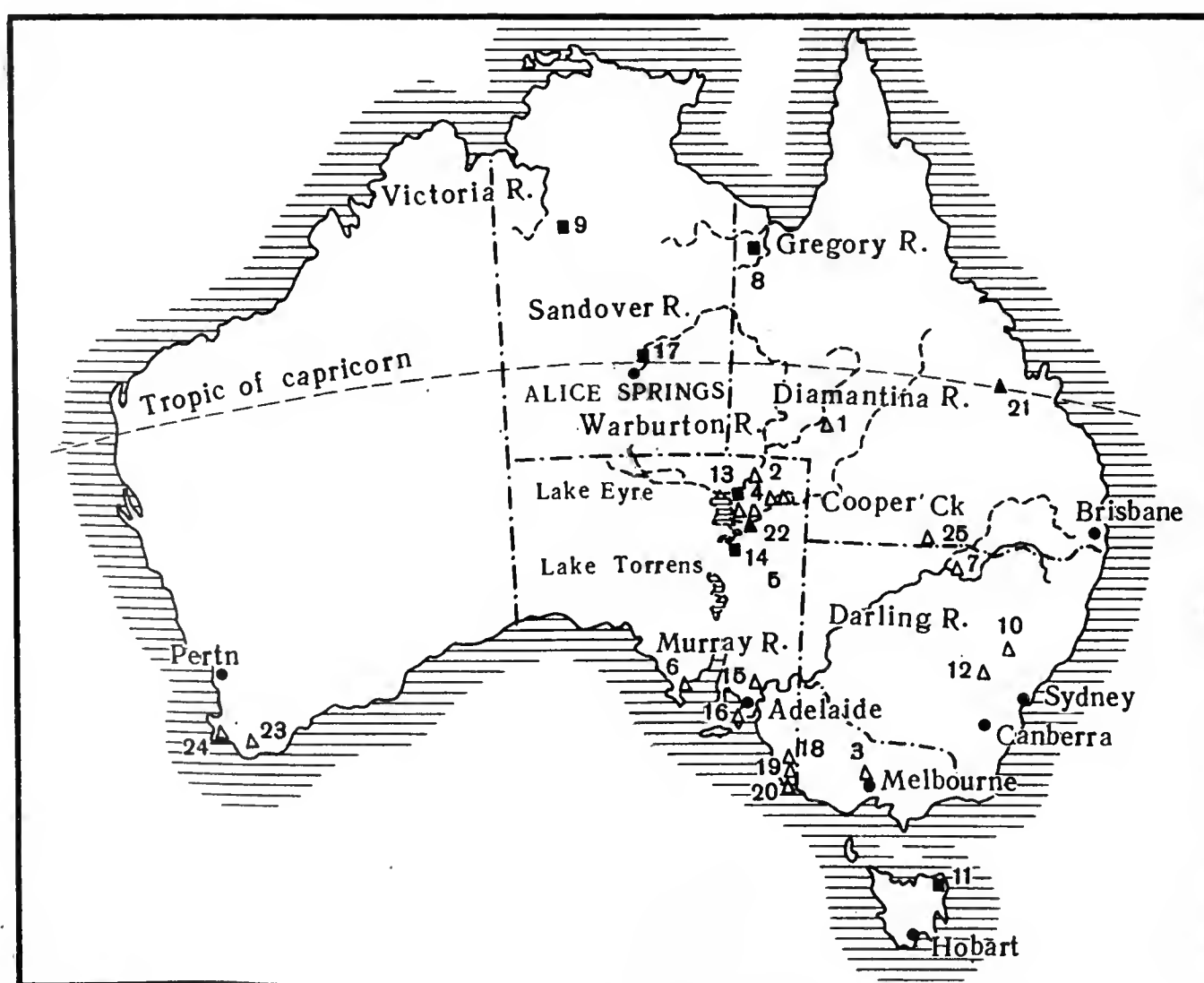
A fragment (30 x 40 mm) of a very large eggshell (4 mm thick) has been recovered from probable Miocene sediments at Snake Dam, near Marree, South Australia. Based on measurements collected by Williams, the minimum egg width was about 126 mm, but length could not be determined. The shell has a rugose outer surface consisting of subparallel ridgelets and slit-like pore openings that are aligned along the longitudinal axis of the egg (Williams, pers. comm.). This is comparable to the linear alignment of pore pits found on eggs of the Malagassy elephant birds (e.g. Aepyornis), emus (Dromaius, Genyornis (Williams, 1980), and moas (Dinornithiformes).



F i g. 11. Stratigraphic distribution of the Dromornithidae in Australia(after Rich, 1981b)

Gizzard stones are common in many localities but are best represented at Lake Callabonna where masses from entire birds are preserved. One associated mass from Genyornis newtoni weighed 14 ounces (=0.4 kg) and consisted of several types of stone (jasper, siliceous sandstone, claystone, quartz) (Stirling, Zietz, 1900).

The greatest diversity of the dromornithids (4 genera, 6 species) is in the Miocene, shortly after they appear in the record (Fig. 11), which suggests



F i g. 12. Geographic distribution of Dromornithidae in Australia (after Rich, 1980)

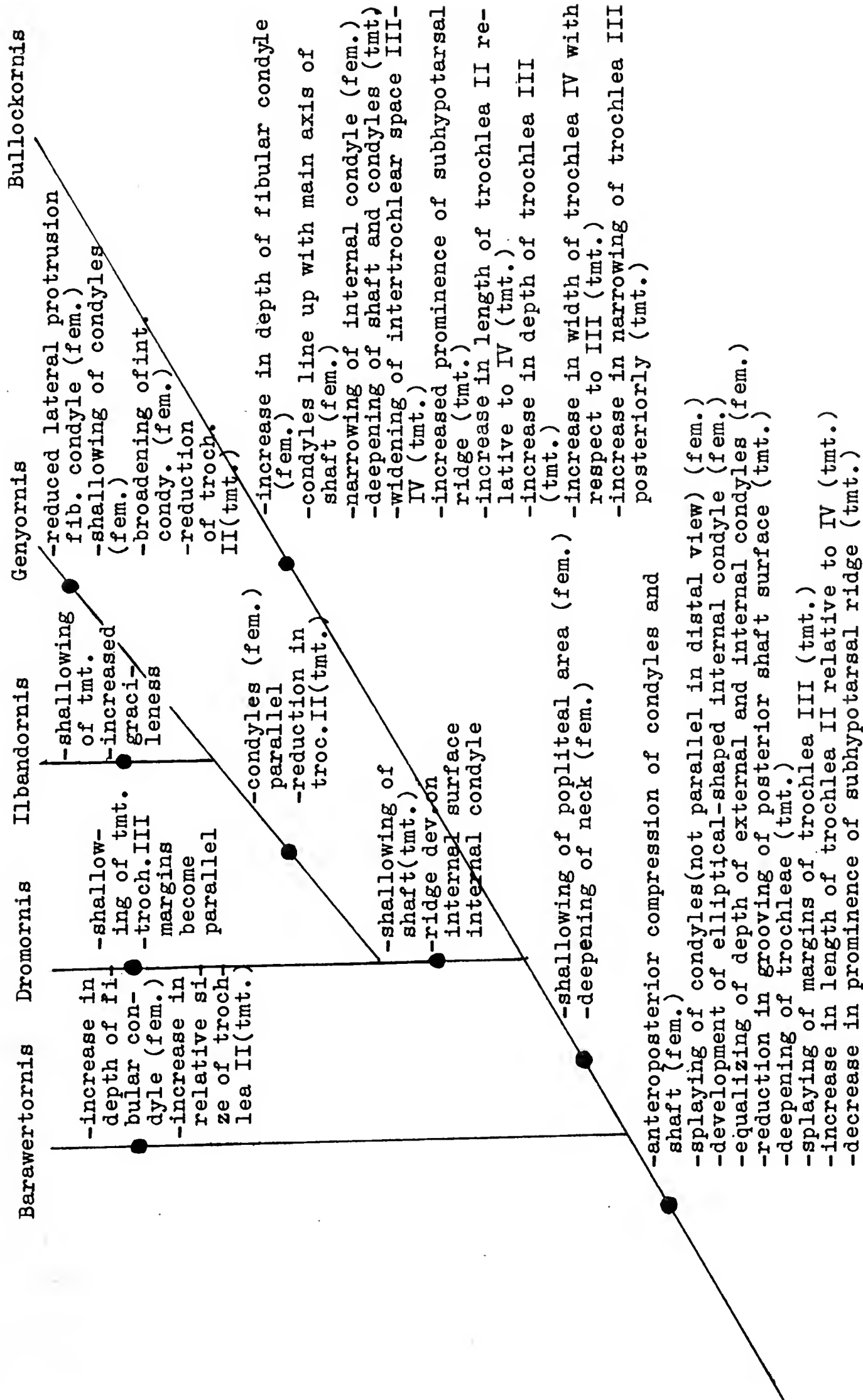
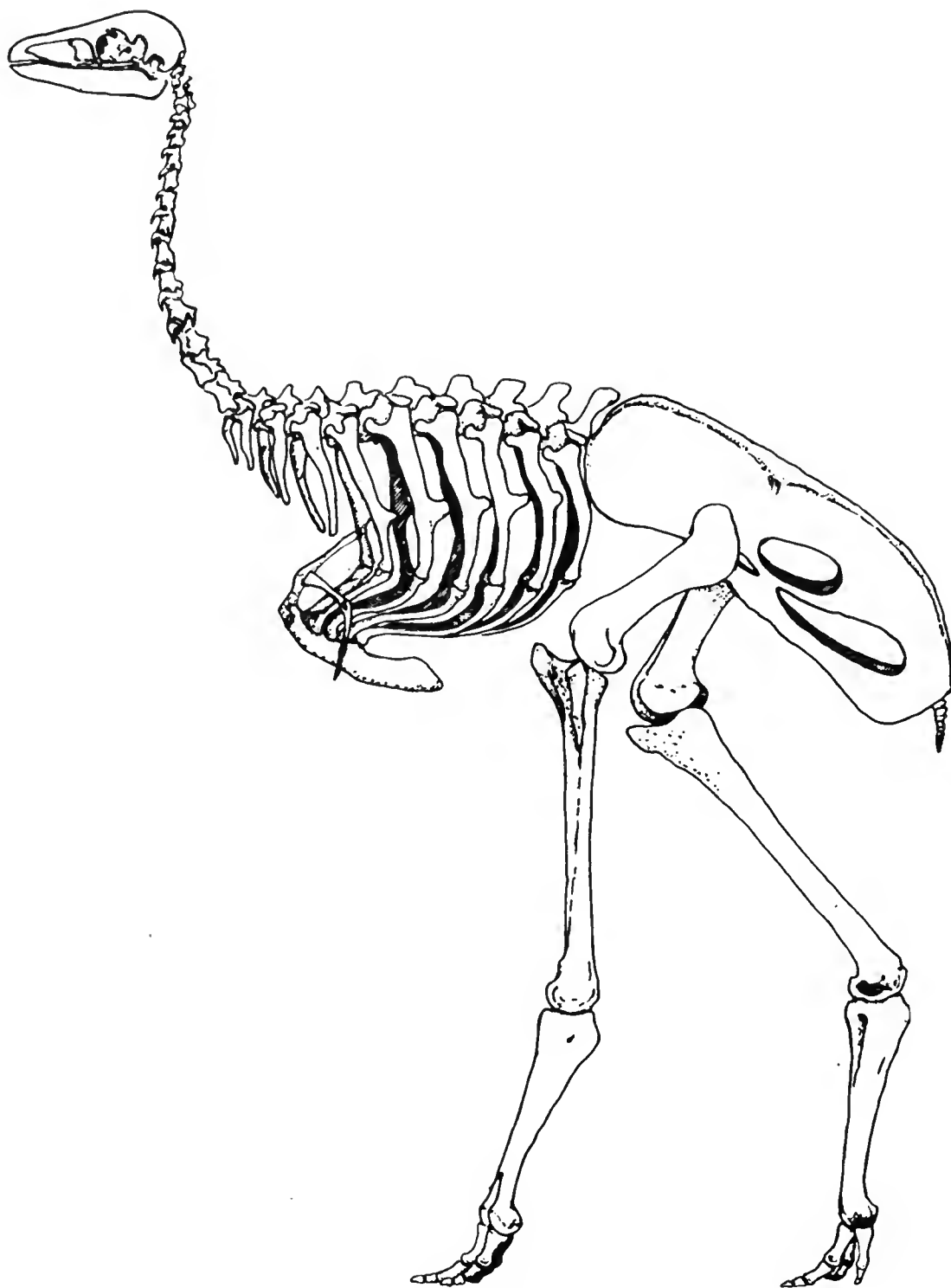


Fig. 13. Proposed morphologic trends within the Dromornithidae (after Rich, 1979c, 1980)



F i g. 14.

Skeleton of Genyornis newtoni from Pleistocene lake sediments at Lake Callabonna, where the most complete dromornithids are preserved (after Rich, 1979c; drawing by H.Galiano)

a much longer history than is recorded at present. In both the Pliocene and Pleistocene only one species (Dromornis australis in the ?Pliocene) Genyornis newtoni in the Pleistocene) are recorded. In the Miocene faunas both graviportal (Dromornis) and cursorial (Ilbandornis) forms existed, demonstrating that divergence in lifestyles was occurring. It seems, however, that the dromornithids were not particularly successful at invading the open-grassland environment, perhaps losing out to emus and kangaroos that radiated in this environment with the increasing aridity in the latest Neogene and Pleistocene, which became extreme about 0.7 million years ago (Hope, 1980).

The main trends that occur in the Dromornithidae are few, although particular taxa seem to have restricted occurrence in time and space (probably somewhat due to the restriction in number of sites). Trends that do occur are, from oldest to youngest, (1) reduction in the size of digit II; (2) increase in size of digit IV until nearly the size of digit III; (3) an increase in the side to side compression of the proximal end of the cnemial crests of the tibiotarsus; and (4) increase and decrease in overall size, amongst others.

Pelecanidae - Pelicans

The pelicans have a long history in the terrestrial (but not marine) deposits of Australia, first appearing in the early Neogene faunas of Central

Australia. The oldest species, Pelecanus tirarensis, is known from the early Neogene sediments producing the Ngapakaldi, Pinpa, and Kutjamarpu faunas in both the Lake Eyre and Tarkarooloo subbasins. This record is based on five fragmentary specimens, but these demonstrate that in the morphology of trochlea II of the tarsometatarsus, this species is distinct from all others (Miller, 1966; Rich and van Tets, 1981). Two other species, both from the Pleistocene are known, also restricted to these central Australian basins (see Maps) and include a small form (P. cadimurka) and the living Australian Pelican (P. conspicillatus). A larger pelican, now extinct, was also present in New Zealand P. novaezealandiae. Pelecanus proavus reported by De Vis (1892) from the Quaternary deposits at Darling Downs in Queensland has been lost, and it is impossible to determine from the illustrations if this tarsometatarsus rates separation as a unique species. Pelecanus validipes (De Vis, 1894 in Brown), part of the Archaeocynus lacustris material reported on by De Vis (1905) and P. grandiceps (De Vis, 1905), all seem to be synonyms of the living Australian pelican (Rich, van Tets, 1981).

The trends evident in pelican morphology can really only be observed on the distal end of the tarsometatarsus on the fossil, as that is the only element preserved that has any time dimension. (1) Trochlea II increases in width along its posterior border; (2) there is both increase and decrease in size; and (3) minor details of shaft and trochlear morphology change.

Palaelodidae

Very like flamingoes in general appearance, although bones were excavated several years ago, this group has only just been recognized in Australia. Unlike the phoenicopterids in Australia, the palaelodids have short tarsometatarsi and very long tibiotarsi as well as characteristic arrangement of the hypotarsus. The palaelodids are thus far known only in the Miocene-aged Etadunna Formation, Ngapakaldi fauna, of Lake Palankarina and are interesting because they have up until now been found only in Europe (Miocene) and North America (Miocene and Pliocene). Obviously, at this time interchange of flying forms between Australia and the Old World was underway. Bats from the Miocene of Riversleigh, N.T. (S. Hand and M. Archer, pers. comm.), also very similar to European forms, reinforce this idea.

Phoenicopteridae - Flamingoes

There are no historic records of flamingoes in Australia other than those in zoos. In the Quaternary, deposits of northeastern Australia bones have been found of what appear to be four species of flamingo. In size they range from: smaller than any extant species; similar in size to the Lesser Flamingo, Phoeniconaias minor; similar in size to the Greater Flamingo, Phoenicopterus ruber (some of which Miller, 1963, indeed assigned to Phoenicopterus ruber; to larger than any extant species.

These are currently under review by Rich and van Tets, and it seems that all or part of material assigned to the following De Vis names are flamingoes: Ibis conditus (holotype), Ocyplanus proeses (holotype), Xenorhynchopsis minor (holotype, and some referred material, and Xenorhynchopsis tibialis) two of the syntypes. Some of these names may be senior synonyms of Miller's (1963) Phoeniconaias gracilis.

All of the Pleistocene material is restricted primarily to interior Aust-

ralia, mainly along Cooper Creek, Kallakoopa Creek, and Lake Kanunka in the Lake Eyre Subbasin, but none have been reported from coastal sites even though the Pleistocene record is extensive. As long as the lakes in this area have water all year long and there were predictable breeding and feeding ground, flamingoes survived. During the latter half of the Quaternary as the "oscillatory mode of extreme climatic fluctuations became established" (Hope, 1980) and the seasonal dryness of the Pliocene savanna conditions gave way to extreme aridity, the flamingoes probably at this time went extinct. Other birds, such as stilts and some ducks were able to survive in the same areas which the flamingoes had found inhospitable, even though birds in those groups had many similar habits, because they could move into other marginal environments and delay breeding until times became good again in the Centre.

Just as during the Pleistocene, flamingo diversity was also high throughout the Tertiary record of this group. Flamingoes first appear in the Miocene fluviatile and lacustrine deposits of the Lake Eyre and Tarkarooloo subbasins. Miller (1963) described the first of this material establishing several new taxa: Phoenicopterus novaehollandiae and Phoeniconotus eyrensis, from the Miocene Etadunna Fm. in the Lake Eyre Subbasin.

Phoenicopterus novaehollandiae according to Miller (1963) differed from other flamingoes in that it had a well developed scar for the metatarsal I, the distal tarsal foramen apparently did not perforate the plantar surface and was situated more proximally on the anterior surface, trochlea IV lay closer to trochlea III, and the posterior extension of trochlea II was narrower mediolaterally and proximodistally (all when compared with Phoenicopterus ruber, the living Greater Flamingo, which is of similar size). Comparisons with fossil flamingoes, including those of the European Aquitanian Phoenicopterus croizeti, led Miller to retain the Australian form as a separate species, albeit similar in size and proportions to the largest flamingo alive today.

Phoeniconotus eyrensis, based on part of a tarsometatarsus and a few phalanges, is of similar size to Phoenicopterus ruber and thus P.novaehollandiae of which it is a contemporary. In fact, the two fossil forms occur in the same geographic area in the Lake Eyre Subbasin. Although in linear dimensions not significantly larger, P.eyrensis was decidedly more robust, and furthermore, according to Miller (1963), differed in a number of morphological features which indicate it had a very large hind toe (I). Miller compared P.eyrensis with the Palaelodidae but found "no significant approach to or link phyletically with the massive, relatively shorter-legged flamingoes" of this family.

All of Miller's material together with a rather large collection of new material recovered from several localities at Lake Palankarinna in the Lake Eyre Subbasin and Lake Pinpa and Eurinilla Creek in the Tarkarooloo Subbasin is being studied by Rich and van Tets. Flamingoes are also known in the late Miocene or early Pliocene fluviatile sediments at Alcoota in the Northern Territory near Alice Springs. All the material, just as in the Pleistocene, appears to be confined to Central Australia.

Examination of this material suggests that mid-Tertiary Central Australia had a diverse and highly endemic flamingo fauna with several species in-

habiting the same geographic areas and sharing these with another flamingo-like group, the Palaelodidae, until recently only known from Europe and North America.

The flamingoes, because of their abundance, diversity and long record, have excellent biostratigraphic potential.

Aegothelidae - Owlet Nightjars

Also known from Pleistocene deposits (e.g. Russenden Cave), this group is represented by a well dated mid-Tertiary form, which is a nearly complete skeleton, Quipollornis koniberi (Rich, McEvey, 1977, Fig. 50). Preserved in a caldera lake deposit in the Warrumbungle Mountains of New South Wales that is overlain by the dated Warrumbungle volcanics (13.5-17 million years old), this specimen gives an excellent view of the "stage of evolution" of the aegothelids at this time during the Miocene.

Although Quipollornis is truly an owlet-nightjar, it is also primitive within that family, a phenomenon often observed in mid-Tertiary birds on a world-wide scale. Although there are some minor differences in the morphology and relative sizes of the jugals, coracoids, scapulae, carpometacarpi, the main differences lie in limb proportions. Quipollornis had longer wings relative to shorter hind limbs, which is more characteristic of the non-aegothelid caprimulgiforms, especially the Caprimulgidae. Such proportions suggest that emphasis on lengthening the hind limb and terrestrial lifestyle had not begun at this time, and this aegothelid was an aerial, rather than a terrestrial, insectivore.

Passeriformes - Songbirds

A variety of small passerine bones has been found in cave and midden deposits of southern Australia, but only a small fraction has been determined to species, and these have been extant species. The main hindrances to identification of bones of birds in this group is the extreme uniformity of birds in this order (mostly exhibiting very small differences from one family to the next) and the lack of complete enough comparative collections. R. Baird (Monash University) is beginning a long term osteological study of the Australian passeriforms that should result in significant advances within fossil groups of this order.

Passeriforms are by no means restricted to the Pleistocene but appear within the first avifaunas known from Australia in the Miocene. Both the Etadunna Formation at Lake Palankarina, the Namba Formation at Lake Pinpa, both in the Great Artesian Basin of South Australia, and the Carl Creek Limestone of Riversleigh, all of Miocene age have produced small passeriform bones. Although the record is too incomplete to be useful biostratigraphically, it may be very useful in determining phylogenetic patterns within this group.

THE QUATERNARY RECORD AND EXTINCTIONS OF AUSTRALIAN AVIAN TAXA

The Quaternary record of birds in Australia is characterized both by extinction of certain taxa as well as gigantism in a number of species. The tally of forms affected by extinction during the past 2 million years is, however, much lower than thought a decade ago. Many of the Pleistocene forms thought to be extinct now, and originally described by C.W. De Vis, appear

upon review to be indistinguishable from extant species (e.g. Olson, 1975, 1977; Rich, van Tets, 1981; Rich, van Tets, McEvery, 1982; van Tets, Rich, 1980).

Several taxa went extinct in Australia during the Quaternary including a mihirung, at least two emus, a cassowary, a penguin, a pelican, a darter, at least two megapodes, three or four flamingoes, and a cuckoo. All of these are long birds, and many are the largest known in their families.

Just what factor or factors brought about the extinction of these forms is quite unknown in many cases, whereas in other cases it is perhaps explainable. Because most Pleistocene sites do not have good absolute dates were synchronous or not, which further hampers interpretation of the causes. The youngest firm date at present on any of the now extinct Pleistocene avifauna is 26.000 years B.P. from Lancefield in Victoria where one species of dromornithid occurred. Whether synchronous in time of extinction or not, one common factor that most of these groups share, is that not only were they affected by extinction but they were, likewise, affected by gigantism.

Some extinctions can be tied to the drastic climatic fluctuations that occurred in the late Pleistocene, which led to the marked dessication of central Australia, the final drying up of the interior freshwater lakes. The flamingoes, and probably pelicans, darters and cormorants, were perhaps thus affected. The marked aridity and unpredictable climatic patterns may have been the final straw for the Dromornithidae, too, as this group was already substantially reduced in diversity at the beginning of the Pleistocene.

Extinctions of the large herbivorous birds and marsupials may be the explanation for loss of the large (and yet unpublished) birds of prey (Accipitridae). What brought about the demise of the other groups, man or climate, or both, has yet to be resolved, and will be difficult to establish until more dated, and carefully excavated sites are known.

ORIGIN OF THE AUSTRALIAN AVIFAUNA: DISPERSAL, VICARIANCE, OR BOTH?

Since P.L. Sclater divided up terrestrial biotas of world into a series of biogeographic regions, there has been much discussion and no too few heated debates about how such units originated. As knowledge of the fossil record of many of the living organisms (upon which Sclater's units were based) was better documented, it became quite obvious that biogeographic regions had certainly changed over a period of time, they were not today what they had been in the past. Even with this realization, however, for the first few decades of the 20th century, most biogeographers were content to move their animal (and plant) pawns on a static geographic "chessboard", that is, the present day arrangement of continents and oceans. It wasn't until the early 1960's that they began to seriously entertain the concept that the "chessboard" may have rearranged its patterns of "squares". With this latter possibility admitted, the biogeography game became complex indeed, and often multiple hypotheses could be invoked to explain distribution patterns.

Most work prior to the 1960's that dealt with origin of the Australasian avifauna, suggested that birds entered Australia from the north across the Malay Archipelago in a series of waves, a valuable concept put forward by

Mayr in his classic paper on the birds of Timor and Sumba (1944a). Mayr was working with a static, not mobile, geography, and his five waves of immigrants were arranged, oldest to youngest, according to how endemic to Australia or how similar to birds of S.E. Asia the birds in question were. He characterized these waves as:

1. Dromaiidae, Casuariidae, Megapodiidae, Loriinae, Cacatuinae, Platycercinae, Podargidae, Menuridae, Atrichornithidae, Grallinidae, Artamidae, Neosittidae, Meliphagidae, Struthideinae, Ptilonorhynchidae, and Cracticidae. (Old endemic families, sub-families, near relatives uncertain).

2. Pedionomidae, Ptilinopinae, Pachycephalinae, Sphecotheridae, Cinclosomatinae, Acanthizinae, Pardalotinae, and Paradisaeidae. (Families and sub-families that are clearly related to Old World families).

3. Numerous genera which are endemic in "Australo-Papua" but which are clearly related to Asiatic genera (e.g. Synoicus, Geopelia, etc.).

4. Numerous species that are clearly related to Old World species (e.g. Coturnix pectoralis, Elanus axillaris, etc.).

5. Numerous sub-species that are in the same species as old world forms (\approx 40 species).

Mayr suggested that group 1 represented the oldest colonists, which arrived in the early Tertiary (or possibly earlier), group 2 arrived in the early or mid-Tertiary, group 3 in the Miocene or Pliocene, group 4 in the Pliocene or Pleistocene, and group 5 very recently. At the time Mayr wrote his paper, there was little palaeontological data to test this hypothesis against, and still there is little fossil information older than Miocene that bears on this hypothesis. One set of fossils that have been found since Mayr's paper, are the early Cretaceous feathers from Koonwarra, Victoria. These simply record the presence of birds in Australia very early on and suggest that this group had a long and independent history on this continent, not necessarily entirely dependent on outside recruitment.

In the early 1960's, biogeographers were faced with a new paradigm a new set of possibilities that must be considered in any study of palaeobiogeography. Seismologists, structural geologists, marine geologists, and geophysicists threw their support behind the concept of continental mobility and such theories as continental drift, sea floor spreading, and plate tectonics were proposed. To the palaeobiogeographer, this meant consideration of at least two possibilities to explain past distribution patterns of their organisms; (1) dispersal on the present day geography with the variability of sea level and appearance and disappearance of land bridges; (2) dispersal and vicariance on a mobile geography which allowed for land bridges to be formed and broken, whole biotas to be transported alive (Noah's Arcs of McKenna, 1974) or as fossils (Viking Funeral Ships of McKenna, 1974) from one continental area to another where they could be cut off from or merged with similar or different biotas. The concept of vicariance attempted to explain distributions of certain organisms by assuming a once continuous population that was split by "continental drift"; and in the opposite direction it meant that related fauna (or flora) that was now separated by a barrier (such as an ocean) could be used to infer previous continuity of the two continental blocks.

As a result of the proposal of these several theories of past continental

mobility several papers, many of a summary nature, were produced, some dealing directly with the origin of the Australian-Australasian avifauna (Cracraft, 1974, 1973, 1980; Keast, 1971, 1972, 1981, 1982; Rich, 1973, 1975 a-b, 1976, 1981, 1982; Schodde, 1980; Schodde and Calaby, 1972; Serventy, 1973). The general outcome of these papers has been a bit confusing, in that some workers strongly support a Gondwanan origin for many bird groups as well as a Southeast Asian origin for others. Some workers still wish to derive all of Australia's avifauna from the north (but these workers are getting fewer and further between). Still other workers are not certain where to derive the birds from. Such lack of a consensus among biogeographers, we think, clearly reflects the nature of the yet unsolved problem of place of origin. Until a good fossil record is at hand, place of origin of many of Australia's birds will remain controversial.

Rich (1975a) divided Australia's non-passeriform avifauna into two groups, one which probably utilized the Indomalaysian route to move between Australia and the rest of the world and a second whose route was uncertain:

Indomalaysian Route (primarily southward movement):

Podicipedidae, Anhingidae, Ardeidae, Ciconiidae, Anatidae, in part (Cyg-nini, Tadornini, Anatini, Aythiini) Accipitridae, in part (Elaninae, Circi-nae, Accipitrinae), Pandionidae (?N or ?S movement), Falconidae, Phasianidae, Gruidae, Rallidae, Otidae, Jacanidae, Charadriidae, Arenariidae, Phalaro-pididae, Scolopacidae, Glareolidae, Laridae, in part (Larinae), Cuculidae, Strigidae, Tytonidae, Caprimulgidae, Hemiprocnidae, (?N or ?S), Apodidae, Alcedinidae, Meropidae, Coraciidae, Bucerotidae.

Route uncertain (Antarctic, Indomalaysian, and in some cases oceanic disper-sal possible):

Casuariidae, Dromornithidae, Pelecanidae, Phalacrocoracidae, Anatidae, in part (Anseranatidae, Cereopsini, Dendrocygnini, Oxyurini), Accipitridae (Mil-vinae, Perninae), Megapodiidae, Turnicidae, Haematopodidae, Recurvirostridae, Burhinidae, Laridae, in part (Sterninae), Rostratulidae, Pedionomidae, Colum-bidae, Psittaciformes, Podargidae, Aegothelidae.

Cracraft (1972) had already suggested that many of the groups in Rich's "Route Uncertain" group, such as the Dromornithidae, Casuariidae, Megapodiidae as well as some suboscine passeriforms and penguins utilized the Gondwana configuration to aid in dispersal to or from Australia - either across the landmass itself or along its margins in the shelf seas.

Certainly these ideas have appeal, especially when near relatives can be found on various fragments of Gondwana. Olson and Steadman (1981) have pointed out the close relationship of the Pedionomidae (Plains wanderers) of Australia and the Thinocoridae (Seed snipes) of South America. One interpretation of this data could be that their present distribution reflects a vicariance event; their common ancestor lived on Gondwana (or part of it) and with the break in communication between Australia and South America some time in the Eocene, the two populations "drifted" apart evolutionarily. Another interpretation, which is also quite possible, although perhaps not as appealing, is that these two families are relicts of a group that was once more widely distributed and has been replaced by another taxa in the northern regions. Because the fossil record of both these groups is known only into the

Quaternary, it is, as yet, not helpful in resolving this dilemma.

Multiple hypotheses, on area of origin and dispersal history, likewise, have been put forward for the Megapodiidae. Cracraft (1972) supports a Gondwana dispersal, and both Olson (1980) and Rich (1975a) are unwilling to make a decision on the basis of current evidence. They feel that the present distribution, and what little is known of the fossil record, could be interpreted using either Gondwanan vicariance or an Indomalaysian dispersal route.

Schodde (1980) and others have more recently suggested that perhaps all of the Caprimulgiformes, the vanelline plovers, the cuculine cuckoos, tytonid owls, and perhaps even the Australian warblers, wrens, babblers, treecreepers, robins, flycatchers and butcherbirds, may have a Gondwanan origin. To this should be added, of course, the lyrebirds (Menuridae) and the scrubbirds (Atrichornithidae) and perhaps the pewees (Grallinidae) and their near relatives. Here, again, however, the basis for denoting such groups as of possible Gondwanan origin is (1) endemic nature; (2) nearest relatives not clearly Old World. Unfortunately, so far, the fossil record of birds in Australia, Asia, Antarctica and South America is not sufficiently long enough and or diverse enough to properly test any biogeographic hypotheses. The record in North America and Europe is quite good, but to adequately test any biogeographic hypothesis regarding the Gondwana continents, a good record there is necessary. Recent discoveries of terrestrial fossil vertebrates on Seymour Island in West Antarctica, as well as the continuing discoveries of new fossil birds in Australasia, Africa, Asia and South America indicates that this task is not impossible but of a long term nature.

So, at present, we are left with several, a minimum of two, hypotheses for the explanation of where many of Australia's birds come from. One hypothesis is that terrestrial birds moved back and forth across a Gondwana landmass, the second is that they utilized an Indomalaysian route. Those groups with low diversity in Australia, high diversity in the Old World, and specific or even generic identity between the two areas, seem very likely candidates to have used the Indomalaysian route, probably moving south across it. Other groups are not so simple to interpret, and even though an individual researcher may have a "gut feeling" for which way the birds moved on which route, at present it is difficult to be certain which hypothesis is correct. Such groups as the Casuariidae, Dromornithidae, Megapodiidae, Pedionomidae, many Psittaciformes, Columbidae, Caprimulgiformes, and many of the Australian Passeriformes are good candidates for having used a Gondwanan route: they are highly endemic, near relatives may be present in South America, relationships to extra-Australian taxa are at higher taxonomic levels (not at the species or generic level). But, until a better understanding of their relationships to other taxa is thoroughly documented and even more importantly, a better fossil record is at hand, speculation will be the state of the art. One needs a good fossil record to document whether, indeed, parsimony is the best explanation for what really happened.

SUMMARY AND CONCLUSIONS

The Australian fossil record of birds begins in the early Cretaceous, but is not good until the Miocene. Miocene samples are mainly from fluviatile sediments and thus highly biased towards medium-sized to large birds that frequent wetland environments.

Only a few groups of birds are useful biostratigraphically in the Australian sequences, and these include the Dromaiinae (emus), Dromornithidae (mihirungs), Pelecanidae (pelicans), and Phoenicopteridae (flamingoes). Upon further examination such groups as the Phalacrocoracidae (cormorants), Anatidae (ducks), Burhinidae (stone curlews or thick-knees), and Rallidae (rails) will also be useful. The record of the remaining groups, although it may be excellent in the Pleistocene, does not have enough time depth to be of great biostratigraphical value yet.

Climatic change, evidently tied to the northward drift of Australia during the Cenozoic, has effected the avifauna of this continent, as has the drift itself. Several groups of birds that prospered in the wetter, more forested conditions of the Miocene and perhaps early Pleistocene of central Australia went extinct in the Pleistocene when rather unpredictable climatic fluctuations became the norm producing the truly arid conditions characteristic of today (e.g. Dromornithidae, Phoenicopteridae). Perhaps man, as well, had an effect on the final extermination of such groups as the Dromornithidae and giant Megapodidae, for there was certainly time overlaps, but this interaction is yet to be documented. The record of extinctions during the Pleistocene, however, is not as drastic as previously thought (about 15 species on present count), because many of the extinct species erected by C.W. De Vis in the late 19th and early 20th centuries have proved to be indistinguishable from extant forms today.

Because of the relatively short good record of birds in Australia, it is difficult at present to speculate with conviction and confidence on where the different characteristic forms of this continent arose. At best, if honest one could say that Australia's avifauna has a multiple origin, having been derived from an ancient Gondwanic beginning, followed by evolution in isolation, leading into an Indomalaysian interchange with Eurasia. Some groups clearly dispersed south along the Indomalaysian route. The others can often be rationalized by either of many hypotheses: dispersal across Gondwana with origin in or outside of Australia, dispersal across the Indo-Malaysian route with origin in or outside of Australia. Better understanding of avian relationships and even more importantly a good fossil record is needed to resolve this "exultation of theories". It is difficult to give up a theory such as that of Mayr, which offers one solid solution concerning Australia's avifaunal origins. It doesn't feel good giving it away for the uncertainty of multiple hypotheses. But it is necessary to do so if our interest is in finding the closest approximation of the truth.

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THE PROBLEM OF MORPHOLOGICAL LEVELS
IN ORGANIZATION OF VERTEBRATES

E.I. Vorobyeva

Institute of Evolutionary Morphology and Ecology of Animals of the
USSR Academy of Sciences, Moscow, USSR

The problem of vertebrate morphological organization levels is closely connected with questions of their structural type formation which determines the "similarity of pattern in members of the same class" (Darvin, 1882, p. 414). The idea of vertebrate structural type stability since the moment of adaptive radiation is still persistent in palaeontology the Swedish school expressing it in the extreme (Stensiö, Jarvik and others). This idea probably takes its origin from the law Unity of Type introduced in to morphology by Cuvier and explained by Darwin from the positions of natural selection and unity of decent (Darvin, 1882, p. 191).

The new based on the unity of structural types found its reflection in phylogeny (the idea of mono- and polyphylie of groups) as well as in systematics, where they were given a certain taxonomic status. Of the three crossop-terigian structural types - porolepiforms, osteolepiforms, coelocanthid the first two were spread up to tetrapod level (Jarvik, 1960).

The acceptance of structural type stability permitted to narrow the number of objects and their characteristics to single representatives - model or reference forms. This situation persisted in morphology until present and serves the basis for the typological way of thought in systematics. It is convenient for classification and diagnostics but still in the latter case faults of the method can be clearly seen when analyzing big taxons (classes for example).

Model forms used for diagnostics represent the mean reflection of the group as a whole because they demonstrate only a certain level of its morphological organization and structural type. In reality this type includes a number of morphological levels (stages) of feature development - the different (and at the same time similar) states which can be traced in primitive and higher organized taxons. A new level can be reached independently in different phyletical lines - a phenomenon pointing to their affinity (Vorobyeva, 1980).

Today the development of the problem dealing with morphological levels of organization in vertebrates acquires a new meaning in connection with the invasion of transformed cladism ideas (Platnick, 1980) from biosystematics into the field of phylogenetics, evolutionary morphology and evolutionary theory. The cladist supporters state (Thomson, 1981) the coming of the new phase of revolution in views upon the system, geneology and historical development of organisms when Simpson and Mayer (Simpson, 1975; Mayer, 1974) conclusions are being argued by Hennig (1966). As a result the discussion about procedures of phylogenetical constructions (still based on morphological features) is getting more and more intensive. In recent years the knowledge on phylogeny of greater taxons is being revised according to positions of Hennig's phylogenetical systematics (this involves mostly Pisciformes, Pisces and the lower Tetrapods).

Today the evolution of the structural changes in the evolution which is somehow connected with morphological levels has been put in the center of attention. In particular when reconstructing phylogeny this evaluation consists in choosing between the maximum number of features as suggested by the evolutionary systematics or the so called a maximum information features of modern cladists (Wiley, 1981). Though Archeopteryx belongs with birds it features a greater number of similarities with archosaur reptiles and this is used as an example to confirm the last statement. The same is true for crocodiles belonging to the birds sister group (Walker, 1972) and featuring also a greater number of reptile features. The verification of sister group diverging from the general stock is based on the verification of two types of progressive features: a) reflecting their general evolutionary tendencies (synapomorphies) and b) features of difference reflecting divergency - autapomorphies. Thus sinapomorphies in crocodiles and birds considered to be sister groups derived from pseudosuchia are the presence of fenestra pseudorotunda, and the periodic pneumatization (Whetstone, Martin, 1979), the similarity in form and replacement principles of teeth in crocodiles and ancient cretaceous birds (Martin et al., 1980) and other. The choice of particular apomorphies greatly depended upon the material considered and upon the personal approach of the investigator (Ostrom, 1976; Tatarinov, 1980; Walker, 1980).

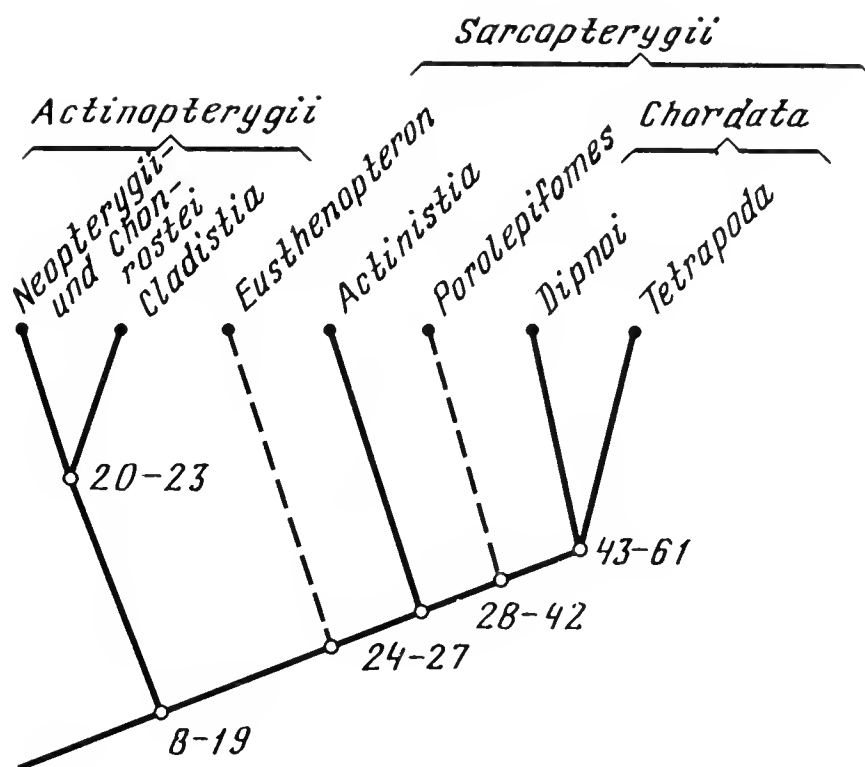
In cases like the one mentioned we deal with the insoluble problems considering the patterns of historical development leading to similar morphological levels in different groups. From the neocladistic point of view this process is somewhat simplified and underestimated for it is reduced to divergent development schemes. Naturally a large number of well known macroevolutionary phenomena and tendencies are not considered (parallelisms, mosaic features, heterochronia), the latter having indisputable influence upon the general pattern of phylogenesis.

Alltogether the neocladistic interest in separate evolutionary results produces grounds for methodological errors. In the first place the continuous and successive properties of morphological levels in evolution is underestimated, because the whole attention is given to a number of identification features. One gets an impression of feature evolution instead of organism and correlative system evolution. The features as well as structure organization states are considered to be static since the difference in evolutionary time scale and mosaic properties of sister groups are ignored. At last the geochronological principle is often left aside and correspondingly the historical approach to morphological levels is underestimated.

Considering the mentioned points we want to stress the dual nature of a morphological level which reflects: 1) on the abscissa - the state of morphological features, which alltogether form the taxonomical status of the group illustrated by reference or model forms; and 2) on the ordinate - the reflection of the historical process of feature formation, which is uneven in time and leads to conservation of primitive states as well as to divergences and parallelisms. It has to be pointed out that although every representatives of the group are being involved in this historical process the degree of involvement differs due to certain variation in natural selection.

The underestimation of the points mentioned leads to doubtful conclusions

Fig. 1. Diagrammatic representation of fish-tetrapod relation (Rosen et al., 1981)



regarding phylogenetic relations as well as tendencies in morphological evolutionary development of groups. Thus the work of American and English ichthyologists (Rosen et al., 1981) presents a revision of views upon fish-tetrapod transition. In particular, the authors consider Dipnoan and Tetrapods sister groups while rhipidistian crossopterygians (the generally accepted Tetrapod ancestors) are being excluded from the number of their possible immediate relatives (Fig. 1). In the present case the succession of skeletal and soft tissue morphology accepted by numbers of morphologists and palaeontologists is ignored completely. The presence of choanae in recent Dipnoan and Tetrapods serves the main argument for stating their alliance. It is also stated that choanae were absent in fossil rhipidistians on the bases of the fact that recent coelocanth-Latimeria has no such feature. But it has been shown recently that coelocanth is only distant relations of rhipidistians. The suggestion of choanae as a synapomorphie was rather a hurried step to take for their homology in the two groups remains unproved (false choanae can be found in actinopterygians and their presence is explained by an adaptation to amphibiotic environments). G.P. Schultze (1981) and American ichthyologist justly noted that in their solving of fish-tetrapod transition problem cladists broke the main rule of phylogenetics when phylogenetical conclusions must be preceded by homology establishment. According to the materials of the 1983 International Symposium "Evolution and Biogeography of Early Tetrapods" the arguments for Tetrapod nature of dipnoan choanas are based on weak grounds. Thus K. Campbell (1983) criticised the interpretation of choanae in a specialized Dipnoan - *Cryphognathus*, used by cladists (Rosen et al., 1981). Apart from that Chang Meemann demonstrated the beginning of posterior nostrils shift on inside the oral cavity in the early devonian primitive Dipnoans from China.

The historical attitude to the evaluation of structural states including the procedure of tracing the process of morphological organization level formation in evolution viewed in geochronological and phyletical succession serve according to Darwin the basis for phyletical unity of structural types. Still neocladists referring to the incompleteness of palaeontological record

often use exclusively the retrospective method of evaluating the phyletical significance of structural states, which naturally increases the possibility of erroneous conclusions. Statements about the recent material being the only one to be used for phylogenetic constructions, the results transferred to palaeontological material only afterwards (Patterson, 1977), reduce the significance of palaeontology for phylogenetics and for the theory of evolution. But according to A.A. Borisiak (1973) palaeontology constitutes the phyletic basis for evolution since it deals with genuine historical documents and new palaeontological finds can at any time put an end to the most logical theory based exclusively on recent material.

The so called transitional or mozaic (De Beer, 1958) forms are of special interest to scientists for they are valuable material for studying the structural changes in evolution and the formation of different morphological levels of organization. Most popular of them are: the Ichthyostega (fish-amphibian transition), the Seymouria (amphibian-reptile transition), Archaeopteryx (reptile-birds transition), Ickhtydosauria (reptile-mammalia transition). Naturally the number of such mozaic species grows together with our paleontological knowledge and the "monster-pioneers" become linked by chains of forms with typical representatives of the lower and upper taxons. Today we know apart from Archaeopteryx other teeth bearing birds from the middle Triassic of Spain, Cretaceous deposits of North America and lower Cretaceous of Mongolia. Along with Ichthyostega come other ancient amphibia from the Devonian of Canada - Acanthostega and Elpistostegia, and a row of stegocephal-like crossopterygians, in particular Panderichthys and Platycephalichthys from devonian continental deposits of the USSR (Vorobyeva, 1977). And the last to be mentioned is the antracosaur with hexadactyle limbs and cranio-shoulder girdle connection, which was recently discovered in the Upper Devonian of Tula region (USSR).

Such mozaic forms apart from presenting extreme cases of heterochronal features in the formation of structural habitas present the characteristic set of features belonging to different morphological levels (structural types) of adjoining taxons.

In particular Ichthyostega had remains of the gill cover and a typical fish tail with Lepidotrichia as well as stegal type of skull and five ray limbs of the level type typical for ancient amphibia.

The influence of mozaic evolution (heterobatism) on the formation of morphological levels can be clearly traced in Archaeopteryx which combines in one both conservative (reptile), progressive (bird) and intermediate features. This set of features easily accounts for the fact that taxonomic status of Archaeopteryx is still unverified: is it a reptile with bird features or a bird (Kurochkin, 1980). Shad (1980) discussed 33 structural properties of this form 21 of which being reptile and 11 bird features. Only 2 features can may turn to be of intermediate nature. According to one group of these features it is a true bird according to another it is a true reptile. Conservative (reptile) features are found mainly in the axial system (cranial features, vertebral column, ribs, sternum, brain, body length). These features (in particular the high lying otico-occipital foramen, long tail, sternum without ca-

rina) lead to conclusions that Archaeopteryx behaved like a reptile when running on the ground: its body orientated in horizontal plane. The analysis of reptile features shows that while some of them are persistent in a number of modern birds (the absence of carina) the others are found in all of them without exception (corneous scales on the legs, symple otic condilum, erythrocytes with nuclei, structure of the jaw joint, one middle ear bone, hard egg shell).

The progressive (bird) features in Archaeopteryx are connected with adaptation to flight and with the vertical orientation of the body. They include feather formation, skeletal pneumatization, changes in limb proportions leading to wing development or to the development of strong legs for bipedal locomotion. Some parallel with Ichthyostega can be traced here: the changes connected with fish-tetrapod transition involved mainly the paired limbs while the fish type of tail together with remnants of gill covers persisted pointing at the close connection with water. Panderichthys - a stegocephal-like fish is also interesting in this aspect. It displays a similar mosaic of primitive fish features (rhomboidal scales, weak differentiation of nasal capsules) together with stegocephal progressive features (distribution of skull roof bones similar to Ichthyostegidae, Labyrinth structure of teeth, stegocephal-like ornament of dermal bones, the seismosensory canals locally open). As in the case of Archaeopteryx it is difficult to understand the mosaic character of features in transitional forms and analogous feature development in the later amphibians without knowledge of early history of rhipidistian crossopterygian evolution as a whole. It is interesting to note that some crossopterygians in the development of certain structures reach the amphibian and even the reptilian morphological level (some features of endocranium, dermal skull bones, teeth etc.) and at the same time as a result of morphogenetic acceleration go even further than the typical state of the group (demonstrated by model form among crossopterygians). This acceleration (Vorobyeva, 1980) can become a property of higher levels that is of amphibians gaining the meaning of a type feature. The resulting morphological resemblance in representatives of different taxonomical groups is based possibly on the similar canalization and related stability of their morphogenetical processes. This stability must probably be displayed mostly in phylatically related and successive groups and thus can serve a certain indicator of affinity in phyla. For instance, as a result of the dermintermedial processes development in the nasal capsule of late Devonian crossopterygian *Platycephalichthys* and *Eusthenopteron* it reaches a state similar to septomaxillary process in different species of recent Anura (Vorobyeva, 1980). This and other examples speak in favour of crossopterygian origin of Tetrapods.

The intermediate features are to be discussed next. Shad (1980) found only two such features in Archaeopteryx and connected them with changes in locomotory pattern and with a tendency towards upright position of the body: 1) tibia and fibula are not fused as in reptiles, but function as one bone like in birds (a change in function comes earlier than the change of form in that case), 2) in adult Archaeopteryx the bones of tarsus are fused proximally (as in birds), but the bones of metatarsus can be actively used when running as

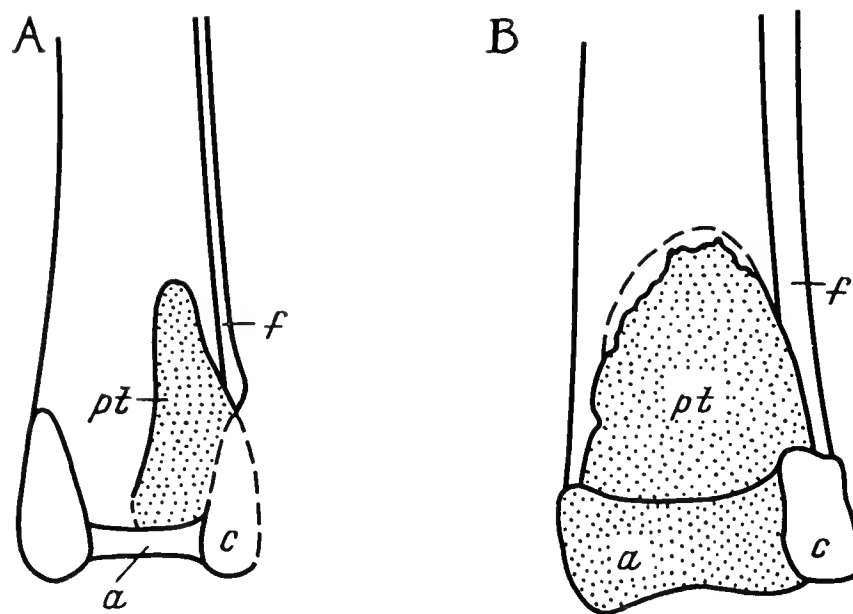


Fig. 2. Parallelisms in the structure of the pretibial bone in Archaeopteryx (A) and Theriodont dinosaur (B). a - astragalus, c - calcaneum, f - fibula, pt - pretibial bone (from Martin et al., 1980)

well as during take off (broadening of functions). The unstable structural features, in particular the intermediate between reptiles and birds can be most effective as a basis for phylogeny. Martin (Martin et al., 1980) showed that the long praetibial bone of Archaeopteryx (persisting in Mesozoan and Recent birds) in spite of its resemblance to the praetibial bone of theropod dinosaurs is not homologous to the latter being an independent ossification connected with calcaneus in its origin (Fig. 2). In theropod dinosaurs the analogous bone presents the product of astragalus. This parallelism in structural changes explained by similarity of function is used as an argument against a dinosaurian hypothesis of bird origin (Martin, 1981).

Probably a similar case of parallelism occurs in the case of choanas in tetrapods, dipnoans and actinopterygians.

Thus we state that 1. The analysis of structural type formation processes in vertebrates is a basis for solving problems of their phyletical connections and for the study of general tendencies of their morphological evolution. 2. The structural organization levels are viewed upon as historical successive stages of structural type formation. 3. The reaching of certain levels of morphological organization (similar stages of homologous organs) occurred rather unevenly in the time scale in phyletically closely related as well as is remotely related groups of common origin. 4. Features of morphological organization of the so called transitional forms standing between large taxons clearly demonstrate the structural type formation in vertebrates. 5. Despite of the gaps in palaeontological record the palaeontological material in several cases gives an opportunity to see the impossibility of homologisation in the absence of fossil forms. 6. The historical attitude (the tracing of evolutionary rows of forms including recent and fossil representatives) has certain advantages before the retrospective attitude. 7. The historical evolution of the recent state of the group gives a possibility to sort out the features belonging to a general level (for instance gnathostomata as a whole) from features specific for this particular group which account for its place and connections in the system.

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NEW DISCOVERIES OF EOCENE AND OLIGOCENE BIRDS IN THE "PHOSPHORITES
DU QUERCY", FRANCE: THE IDIORNITHINAE (RALLIFORMES, CARIAMIDAE)

NOUVELLES DÉCOUVERTES D'OISEAUX EOCÈNES ET OLIGOCÈNES DANS LES PHOSPHORITES
DU QUERCY, FRANCE: LES IDIORNITHINAE (RALLIFORMES, CARIAMIDAE)

Cécile Mourer-Chauviré

Centre de Paléontologie stratigraphique et Paléoécologie de l'Université
Claude Bernard, associé au CNRS (LA 11), 27-43 boul. du 11 novembre,
69622 Villeurbanne, France

INTRODUCTION

Parmi les formes les plus abondantes des Phosphorites du Quercy se trouvent des échassiers décrits sous le nom d'Elaphrocnemus Milne-Edwards, 1891 et d'Idiornis Oberholser, 1899 (= Orthocnemus Milne-Edwards, 1891). Ces genres ont été créés à partir des tarsométatarsiens. A. Milne-Edwards (1891), C. Gaillard (1908) et J. Cracraft (1973) ont proposé de leur attribuer des tibiotarses et des fémurs mais le reste du squelette n'était pas connu. Ces deux genres ont été considérés comme une famille à part, les Idiornithidae, placée tentativement dans l'ordre des Ralliformes, sous-ordre Ralli (Brodkorb, 1967).

En 1891 A. Milne-Edwards décrit également dans les Phosphorites le genre Filholornis, représenté par des humérus, des cubitus et des métacarpiens. Ce genre a été considéré comme voisin du genre actuel Opisthocomus, l'hoazin, et a été classé comme celui-ci parmi les Galliformes (Brodkorb, 1964). Les recherches sur les protéines du blanc d'oeuf ont permis de montrer que le genre Opisthocomus est en réalité plus proche des Cuculiformes et il est actuellement classé dans la famille des Cuculidae (Sibley, Ahlquist, 1972).

Le genre Elaphrocnemus étant très abondant dans les Phosphorites du Quercy, il est difficile de concevoir, si l'on a beaucoup d'os des pattes, que l'on n'ait pas au moins quelques os des ailes. Les nouvelles fouilles n'ont pas permis de trouver réellement des squelettes d'oiseau en connexion, cependant on s'aperçoit que, dans les gisements où l'on trouve des restes de Filholornis, on trouve toujours également des restes d'Elaphrocnemus. Dans certains gisements on a des ossements de Filholornis et d'Elaphrocnemus dont on peut penser qu'ils proviennent du même individu. Je propose donc de mettre en synonymie les genres Elaphrocnemus et Filholornis.

D'autre part, pour le genre Idiornis, on a trouvé une nouvelle espèce de ce genre, de taille supérieure à celle des espèces précédemment connues, et représentée par des os des ailes associés à des os du membre postérieur. Ces éléments de l'aile n'étaient pas connus jusqu'à présent et sont différents de ceux du genre Filholornis.

L'ensemble du matériel recueilli dans les nouvelles fouilles, ainsi que le matériel inédit provenant des anciennes collections, montre que les genres Idiornis et Elaphrocnemus présentent le plus d'affinités avec les genres sud-américains actuels Cariama et Chunga, de la famille des Cariamidae. Ils présentent également des ressemblances avec la famille éteinte des Bathornithidae, connue jusqu'à maintenant seulement en Amérique du Nord et dont J. Cracraft (1968) a également souligné les affinités avec les Cariamidae. En raison de la ressemblance des Idiornithidae et des Bathornithidae fossiles avec

les Cariamidae actuels, j'ai proposé la classification suivante (Mourer-Chauviré, 1981):

Famille Cariamidae Bonaparte, 1853

Sous famille Bathornithinae Wetmore, 1927

Sous famille Idiornithinae (Brodkorb, 1965)

Sous famille Cariaminae Bonaparte, 1853

MATERIALS

Le genre Elaphrocnemus

Le coracoïde a une forme générale mince et allongée; la tubérosité brachiale est très légèrement recourbée vers l'avant et du côté interne; la facette scapulaire n'est pas creusée et mal délimitée; le procoracoïde est très réduit; il n'y a pas de fenêtré coracoïdienne; la facette sternale est mince, peu arquée chez E.phasianus, plus arquée chez E.crex.

L'humérus est connu sous le nom de Filholornis. Il est court et trapu, élargi aux deux extrémités, sa partie proximale est aplatie et recourbée vers l'arrière. Il n'y a pas de fosse pneumatique en dessous de la tubérosité interne, on voit un petit orifice pneumatique qui s'ouvre à la surface de l'os. Par sa forme générale cet humérus ressemble à celui d'Opisthocomus, mais chez ce dernier la tubérosité interne est plus développée, il y a une fosse pneumatique profonde et un large orifice pneumatique.

Le cubitus ressemble beaucoup à celui des genres actuels Cariama et Chunga. Il est très aplati sur la face anconale, l'olécrâne n'est pas saillant vers le haut mais aplati en forme de lame et rejeté sur le côté interne. L'extrémité distale est également aplatie, le condyle interne, très peu saillant, est presque confondu avec le condyle externe.

Le métacarpien est court et massif. Le grand métacarpien est robuste et aplati sur la face interne. Le petit métacarpien très arqué, va rejoindre presque directement l'apophyse pisiforme. Il n'y a pas de tubérosité intermétacarpienne. Le métacarpien alulaire est dirigé presque perpendiculairement à l'axe du grand métacarpien et se termine par un processus arrondi.

Le fémur ressemble beaucoup à celui des Cariamidae actuels. Il est très élargi à sa partie proximale, la tête est fortement en saillie du côté interne, le col étroit et allongé. A la partie distale le sillon rotulien est profond et oblique par rapport à l'axe de la diaphyse, les deux condyles sont bien renflés, le condyle externe est situé nettement plus bas que le condyle interne.

Le tibiotarse est connu et a été figuré par J.Cracraft (1973). La crête cnémiale interne est très saillante vers l'avant, la crête cnémiale externe présente à son extrémité une surface aplatie vers le haut et vers l'avant. La partie distale est élargie transversalement, le condyle interne est plus court et plus saillant vers l'avant que le condyle externe, la fosse intercondylienne antérieure est large.

Le tarsométatarsien est également connu et figuré (Gaillard, 1908; Cracraft, 1973). Ses principaux caractères sont: pas de canal fermé dans l'hypotarse, gouttière étroite et profonde délimitée par deux crêtes dirigées postérieurement; trochlée interne beaucoup plus réduite que la trochlée médiane.

Le genre Idiornis

Le coracoïde a une forme très particulière car le procoracoïde, très développé, rejoint la tubérosité brachiale en formant un anneau complètement fermé. La facette scapulaire est creuse et bien délimitée. La facette scapulaire est creuse et bien délimitée. La fenêtre coracoïdienne se traduit généralement par une échancrure le long du bord interne. La facette sternale est mince, peu arquée, avec un léger épaississement à l'angle interne. La section de la diaphyse est aplatie chez les formes primitives, quadrangulaire chez les formes évoluées. Ce coracoïde ressemble beaucoup à celui des Cariamidae actuels et à celui des Bathornithinae (genre Paracrax).

L'humérus est connu seulement par des extrémités proximales et distales. La tubérosité interne est plus développée que dans le genre Elaphrocnemus, il y a une fosse pneumatique et un large orifice pneumatique. La partie distale est élargie du côté interne, le condyle externe est très en relief, le condyle interne, globuleux, tend à s'allonger du côté interne, les deux condyles sont bien séparés.

Le cubitus n'est pas connu avec certitude. On peut attribuer à Idiornis un cubitus distal qui ressemble à celui d'Elaphrocnemus mais où le condyle interne est plus saillant.

Le métacarpien ressemble beaucoup à celui d'Elaphrocnemus mais chez Idiornis les deux métacarpiens sont soudés sur une certaine distance en dessous de la partie proximale, tandis que chez Elaphrocnemus le petit métacarpien vient se souder partiquement au niveau de l'apophyse pisiforme. Chez Idiornis l'apophyse pisiforme est située très en avant, le petit métacarpien est moins arquée que chez Elaphrocnemus, il est aplati en forme de lame et présente une petite protubérance sur la face interne, à la partie proximale. Le métacarpien d'Idiornis ressemble beaucoup à celui des Cariamidae actuels et à celui d'Opisthocomus.

Le fémur a une forme plus allongée que celui d'Elaphrocnemus, la tête est moins projetée, le col plus épais et moins dégagé. La gorge rotulienne est moins profonde et moins oblique que chez Elaphrocnemus.

Le tibiotarse distal, seul connu, ressemble beaucoup à celui d'Elaphrocnemus mais la partie distale est moins élargie transversalement.

Les principaux caractères du tarsométatarsien sont les suivants: par de canal osseux fermé dans l'hypotarse, gouttière peu profonde bordée par deux crêtes peu saillantes (une crête externe aplatie et dirigée postérieurement, une crête interne un peu plus développée et dirigée du côté postéro-interne) large gouttière métatarsienne antérieure, trochlée interne pratiquement aussi développée que la trochlée externe.

COMPARAISONS

Cariamidae actuels et Opisthocomus

Parmi les formes actuelles, les genres Idiornis et Elaphrocnemus présentent des affinités avec les Cariamidae et avec le genre Opisthocomus. Dans le genre Idiornis le coracoïde, l'humérus, le métacarpien, le tibiotarse et le tarsométatarsien ressemblent particulièrement à ceux des Cariamidae mais, chez ces derniers le tibiotarse et le tarsométatarsien sont proportionnelle-

ment beaucoup plus allongés, Le métacarpien ressemble à la fois à celui des Cariamidae et à celui d'Opisthocomus. Dans le genre Elaphrocnemus le cubitus et le fémur ressemblent très fortement à ceux des Cariamidae actuels tandis que l'humérus rappelle plutôt celui d'Opisthocomus. Cela montre que les formes fossiles présentent parfois des mosaïques de caractères que l'on retrouve actuellement dans des groupes très séparés. Il faut donc être très prudent lorsque l'on veut reconstituer l'histoire phylogénétique d'un groupe d'oiseaux fossiles. Il n'est pas possible de tracer des schémas évolutifs en utilisant simplement un ou deux éléments, mais il faut prendre en considération l'ensemble du squelette.

Bathornithinae

Les Idiornithinae et les Bathornithinae sont considérés depuis longtemps comme deux groupes-frères (Cracraft, 1973). Les Idiornithinae sont connus pour le moment seulement en France, de l'Eocène supérieur à l'Oligocène supérieur, et les Bathornithinae en Amérique du Nord seulement, de l'Oligocène inférieur au Miocène inférieur. J.Cracraft (1973) a effectué une analyse comparée du tibiotarse distal et du tarsométatarsien de ces deux groupes. Cette analyse montre qu'ils sont très proches, la principale différence étant la présence d'un canal osseux fermé dans l'hypotarse chez les Bathornithinae et d'une gouttière ouverte chez les Idiornithinae. En outre A.Wetmore (1933 a,b) signale que les Bathornithinae n'ont pas de doigt postérieur I tandis que les Idiornithinae, comme les Cariamidae actuels, en ont un.

Le reste du squelette confirme la parenté de ces deux groupes. Le coracoïde d'Idiornis est très proche de celui de Paracrax wetmorei, la principale différence étant que chez Paracrax le procoracoïde et la tubérosité brachiale ne se rejoignent pas complètement.

A la partie proximale de l'humérus, le sillon capital forme un angle de 45° par rapport à l'axe de la diaphyse chez Paracrax et chez Idiornis, cet angle est plus petit chez Elaphrocnemus et chez les Cariamidae actuels. A la partie distale la forme générale des condyles est proche. Chez Elaphrocnemus le condyle interne est globuleux et bien séparé de l'entépicondyle, chez Idiornis et chez Paracrax antiqua le condyle interne tend à s'allonger du côté interne, chez P.wetmorei et B.celeripes le condyle interne s'aplatit du côté interne pour former une crête qui rejoint l'entépicondyle. Chez Idiornis la gouttière tricipitale externe est légèrement marquée. Il n'y a pas de gouttière tricipitale chez Elaphrocnemus et chez les Bathornithinae.

Le cubitus d'Elaphrocnemus ressemble énormément à celui des Cariamidae actuels et diffère nettement de celui des Bathornithinae. En effet ce dernier est beaucoup moins aplati sur la face anconale et l'olécrâne ne forme pas une lame aplatie du côté interne. En revanche le cubitus distal attribué de façon incertaine au genre Idiornis ressemble un peu plus à celui des Bathornithinae parce que, comme chez celui-ci, le condyle interne est assez prononcé et la tubérosité carpienne forme une sorte de coin allongé parallèlement à l'axe de la diaphyse.

Le métacarpien d'Idiornis ressemble à celui de Paracrax car il a un processus pisiforme bien développé et situé assez loin vers l'avant. Chez les

Idiornithinae, comme chez Paracrax, la partie de l'os située entre le processus pisiforme et le petit métacarpien est distinctement soulevée. Si l'on prend les autres caractères énumérés par J. Cracraft (1968, p. 36) les Idiornithinae diffèrent des Bathornithinae et sont plus proches des Cariaminae. Ces caractères sont: chez les Idiornithinae le rebord externe de la trochlée carpienne forme un sommet pointu (arrondi chez Paracrax); le métacarpien alulaire est situé plus distalement et dirigé antérieurement; la portion postérieure du rebord interne de la trochlée carpienne est fortement recourbée antérieurement (surtout chez Idiornis); le processus pisiforme est situé encore plus en avant chez Idiornis que chez Paracrax.

Le tibiotarse proximal, connu chez E. phasianus, ressemble beaucoup à celui de B. fricki (Cracraft, 1968; fig. 1 et 1973; fig. 27) par la forme des crêtes cnémiales et les proportions relatives des deux surfaces articulaires. Il y a aussi une crête entre les surfaces articulaires et la crête cnémiale interne, mais elle est moins marquée que chez Bathornis et chez Cariama.

Psophiidae

A l'intérieur des Ralliformes actuels, les Cariamidae sont considérés comme plus étroitement apparentés aux Psophiidae qu'à toutes les autres familles de cet ordre (Cracraft, 1968). D'autre part les Bathornithinae, bien qu'ils possèdent beaucoup de caractères communs avec les Cariamidae actuels et les Phorusrhacidae fossiles, ressemblent aux Psophiidae par la forme de l'extrémité proximale du tarsométatarsien (Cracraft, 1968).

La comparaison de l'ensemble du squelette des Idiornithinae avec celui des Psophiidae actuels permet de montrer qu'ils sont très différents. La seule partie du squelette qui présente quelque ressemblance est l'extrémité distale du tarsométatarsien, mais il y a des différences dans la position du foramen distal, situé plus bas chez Psophia, et dans la présence d'un sillon articulaire sur la face antérieure de la trochlée interne chez Psophia.

CONCLUSIONS

L'étude des Idiornithinae du Quercy montre donc qu'ils sont proches des Bathornithinae d'Amérique du Nord et que l'ensemble Bathornithinae-Idiornithinae est proche des Cariamidae actuels d'Amérique du Sud.

Les relations qui existent entre les faunes d'oiseaux du Quercy et celles d'Amérique du Sud sont soulignées en outre par la présence dans le Quercy d'un Phorusrhacidae (Mourer-Chauviré, 1981). Jusqu'à présent les Phorusrhacidae avaient été signalés seulement en Amérique du Sud, de l'Oligocène au Pléistocène, et en Amérique du Nord, au Pléistocène. La forme du Quercy, Ame-ghinornis minor, représente un oiseau de taille moyenne et dont l'aptitude au vol, quoique réduite, était encore présente.

L'existence de formes voisines dans le Quercy et en Amérique du Sud peut s'expliquer soit par une diversification très ancienne de ces formes, soit par des phénomènes de migrations intercontinentales (Mourer-Chauviré, 1981, 1982). Si l'on admet une diversification très ancienne, on peut penser que

les Cariamidae représentent les restes d'une première radiation de Ralliformes qui se serait répandue dans le continent de Gondwana avant sa séparation en différents blocs. Si l'on admet une diversification plus récente, en Amérique du Sud ou en un autre point de la guirlande gondwanienne, il existe des possibilités de migrations, démontrées par des échanges faunistiques, au Crétacé supérieur ou à l'Eocène, entre Amérique du Sud et du Nord, Amérique du Sud et Afrique, Afrique et Europe, Amérique du Nord et Europe (Rage, 1978, 1981; Buffetaut, Rage, 1982; Mourer-Chauviré, 1982). Il y a donc plusieurs possibilités pour expliquer la présence dans le Quercy des Phorusrhacidae et d'un groupe voisin des Cariamidae actuels. Seule la découverte de nouveaux fossiles, en Afrique particulièrement, permettra de résoudre ces problèmes et d'établir la chronologie des événements.

RÉSUMÉ

De nouvelles fouilles dans les anciens remplissages karstiques connus sous le nom de Phosphorites du Quercy ont permis de retrouver des oiseaux fossiles associés à des faunes de micromammifères et donc bien repérés au point de vue stratigraphique. Dans certains cas il est possible d'associer différents éléments du squelette pour des oiseaux qui n'avaient été décrits auparavant que d'après un ou deux ossements.

Chez les Idiornithinae, les os des ailes décrits sous le nom de Filholornis correspondent aux os des pattes décrits sous le nom d'Elaphrocnemus. Dans le genre Idiornis les différents éléments du membre antérieur jusqu'alors inconnus, montrent que de genre était assez proche des Bathornithinae, oiseaux coureurs qui vivaient à la même époque en Amérique du Nord. Dans l'ensemble la sous-famille des Idiornithinae montre beaucoup de ressemblances avec les Cariamidae actuels d'Amérique du Sud. Enfin quelques restes peuvent être attribués à la famille des Phorusrhacidae, connue auparavant au même âge en Amérique du Sud seulement.

Toutes ces formes montrent que le sous ordre Cariamae était déjà extrêmement diversifié à l'Eocène, et répandu sur plusieurs continents. Sa diversification a probablement commencé dès le Crétacé, peut être dans le continent de Gondwana avant sa séparation en différents blocs.

SUMMARY

New excavations in the sink-hole fillings known as "Phosphorites du Quercy" made it possible to find fossil birds associated with micromammals faunas and, by this means, well located in the chronostratigraphic scale. Besides it is possible, in some cases, to associate the different elements of the skeleton for some birds which were previously known only by one or two anatomical parts.

In the Idiornithinae the wing bones ascribed to the genus Filholornis fit with the leg bones of the genus Elaphrocnemus. In the genus Idiornis the different elements of the upper limb, not previously known, show that they are closely related to the Bathornithinae, cursorial birds, which lived in the same period in North America. On the whole the subfamily Idiornithinae shares many

analogies with the recent Cariamidae of South America. Finally some remains can be attributed to the family Phorusrhacidae which have been known, in this time period, only in South America.

All these occurrences show that the suborder Cariamae was already highly diversified in the Eocene and widespread in several continents. Its diversification probably began in the Cretaceous, maybe in the Gondwanaland, prior to its separation into different continental masses.

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Symposium

SENSORY ORGANS AND COMMUNICATION IN BIRDS

Convener: V. ILYICHEV, USSR

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TEMBROCK G.

BIOCOMMUNICATION IN BIRDS

KHAYUTIN S.N.

ACOUSTICAL AND VISUAL MECHANISMS OF THE NATURAL BEHAVIOUR OF
TREE-HOLE NESTLINGS

WALLSCHLÄGER D.

ACOUSTICAL COMMUNICATION OF WOODPECKERS

GOLUBEVA T.B., TIKHONOV A.V.

THE VOICE AND HEARING OF BIRDS IN ONTOGENY

TEMCHIN A.N.

ACOUSTICAL RECEPTION IN BIRDS

BIOCOMMUNICATION IN BIRDS

Günter Tembrock

Sektion Biologie der Humboldt-Universität zu Berlin,
1040 Berlin. GDR

Biocommunication will be performed via signal systems, evolved during the process of evolution and effective also as a factor of evolution, realized by changes in the pool of genes in populations. Signal systems will be derived from employment systems:

- employment systems control the interactions of an organism with his environment: to warrant the structural and functional properties of the body; to warrant the execution of behavioural patterns in the ecosystem;
- signal systems control the interactions of an organism in the population.

Employment systems include employment behaviour, based upon an informational exchange with the environment, using informative signs or signals. The receiver designates the meaning of informative signs. Signal systems include signal behaviour, using communicative signals. The sender designates the meaning, and this rests upon the possibility of choice on the part of the sender (Lyons, 1972). Only in this context we will use the word 'biocommunication'.

We suggest, that signal systems can be derived from employment systems of behaviour. Receptors had been evolved to secure the metabolic needs and the protection of the body against injuries. In secondary process, these structures and functions will be used to transmit informations between conspecific animals. The emission of such messages will be realized by signalling behaviour; the evolution of these behavioural functions has been called "ritualization". In this process of evolution the three vectors of animal behaviour take part:

- the input vector, build up by the external analysator systems,
- the internal vector as system of motivations, emotions, arousal-states, and general motoric states;
- the output vector as system of all efferences, the control element with respect to the environment.

'Motivation' means the readiness to perform a special behaviour, adapted by evolution and individual experience to the environment with the function, to perform special needs of the organism.

We will give an example:

A passerine bird perceives a raptorial bird in the air. This means for him "aerial enemy". After this process of identification and designation as a function of the input vector, in consequence the internal state of "fright" will be established, that means the readiness for execution of a special behaviour pattern.

This leads in the output vector to a flight behaviour pattern typical for this species. The whole process demonstrates in our description an employment behaviour.

If we accept these general phases of the behavioural interaction with the environment, we can derive three steps of evolution of biocommunicative behaviour processes (Fig. 1):

1. The transmission of the behavioural processes of the output vector, that means a functional transmission. the receiver executes the same beha-

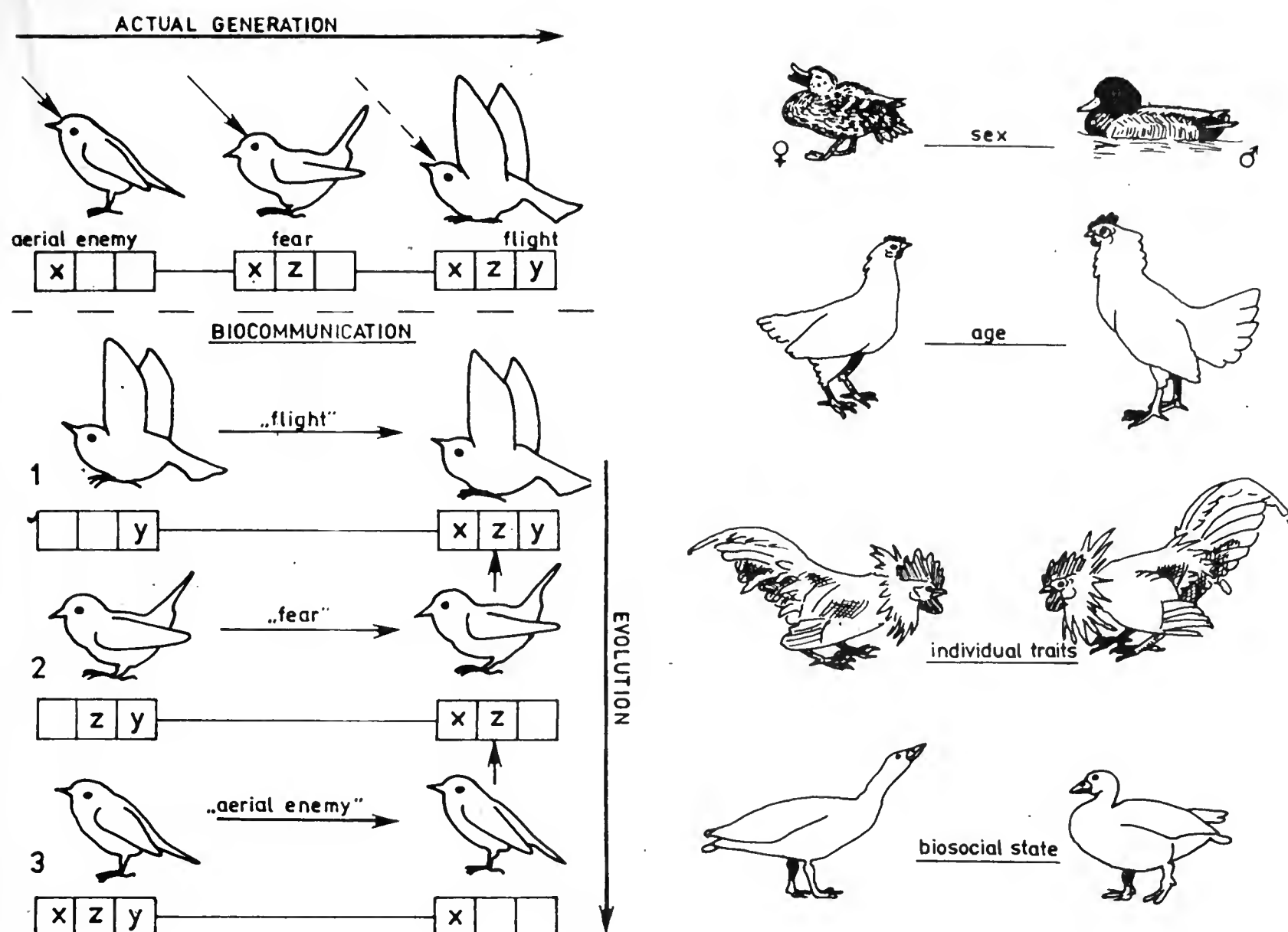


Fig. 1. Three steps of evolution of biocommunicative behaviour processes

Fig. 2. The differences delivering gradients between the partners

viour as the sender, that may be an allelomimetic phenomenon, but it does not include a special internal state. In our example, the "flight" will be transmitted (and this in the double sense of the word). This is only a biocommunicative process, if the sender performs a special pattern of this behaviour, usually in a form of exaggeration.

2. The signals of the sender transmit his internal state, in our example the readiness of flight-behaviour. The signals designate the state of "fright", or what we denominate in this context by this word. The receiver is now in the same state as the sender (but without information about the motive of this state); he may execute a flight behaviour.

3. The signals of the sender transmit informations about the perception of the sender, in our example designated as "aerial enemy", in some birds indicated by special acoustic signs. Now, the receiver is able to react as if the information was performed by himself. In many cases, the mutual exchange of information between sender and receiver leads to a total perception of the primary cause of the biocommunicative behaviour of the first sender. This level of biocommunication build up two principal degrees of freedom in the receiver: the choice of the internal state and the choice of the external behaviour pattern.

Biocommunication controls intraspecific relations, in some cases - especially in sibling species - interspecific processes also. In general these processes will be guided by evolutionary stable strategies. With respect of these phenomena, we see in the 'theory of gradients' a possible evolutionary mechanism. This supposes a common context of the intercommunicating individuals. The communicative integrated individuals build up an adapted system of interactions with the environment. There are three elementary constitutional constituents under these conditions, which deliver gradients between the partners:

- sexual differences, that means the sexual dimorphisms, expressed in several grades,
- differences related to the age of the individual,
- differences related to the individual traits independent of sex and age, insufficiently described by words as 'nervous type' or 'temperament' (Fig. 2).

Such differences are positively correlated with evolutionary processes, determined by K-selection, that means that the quality of the individual produced is a constitutional part of this strategy of evolution with a high parental investment. In such mostly nonanonymous groups, the biosocial state itself may deliver gradients, for instance with respect to biosocial roles as manifested in rank orders. What we wish to say is the following: increase of such gradients within populations or biosocial structures enlarges the possibility of informational needs, satisfied by biocommunication. We find this phenomena with respect to courtship and parental care, and in this context we presume roots of the complexer forms of interactions in biosocial units.

In addition to the gradient, mentioned above, the following conditions operate in the same sense (Fig. 3):

- the spatial distance between the partners of biocommunication,
- the temporal differences with respect to phase-shifts in the level of activity,
- the motivational difference, for example in the level of metabolic needs ('hunger' contra 'satiation'),
- differences with respect to the interaction with the environment.

Therewith some principal possibilities are picked up, which promote the evolution of biocommunicative mechanisms; common for all is the existence of gradients between individuals, which are connected with their environment by common context, to form a pair bonding, to execute parental behaviour, or to benefit natural resources in the ecosystem, or to protect against predators.

This leads to the question: what affect those signals with respect to the receiver. This is a discussion of the ergomatic aspect of biocommunication. This can be regarded in relation to the three vectors of animal behaviour (Fig. 4):

- input vector: signals cause the identification of the sender; signals orientated to the sender;
- vector of internal states: signals promote unspecific excitation; signals effect discrete changes of the internal state, for instance, they activate a special motivation;
- output vector: signals release a special employment behaviour pattern (non-communicative behaviour); signals release a communicative behaviour pattern.

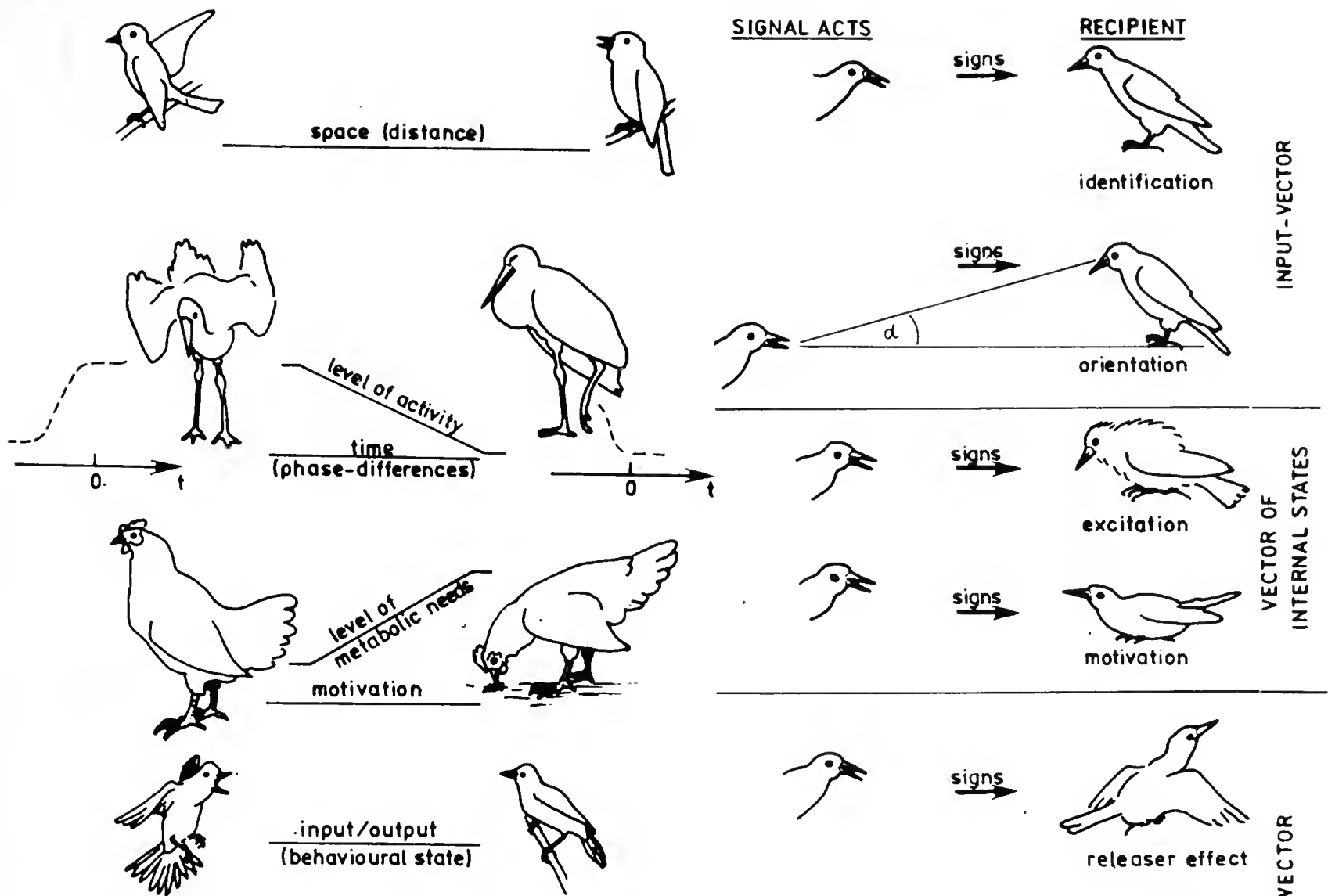


Fig. 3. Some other conditions control intraspecific relations

Fig. 4. Three vectors of animal behaviour

Generally we also may derive the following classes of effects of biocommunicative signals:

- signals modify the motoric state of the receiver in the sense of kinesis (kinesis effect);
- signals modify the state of orientation in space with respect to the direction: taxis effect;
- signals modify the distance between sender and receiver: elasis effect;
- signals modify in the sense of "zeitgeber": chronobiological effect;
- signals trigger a special behaviour pattern: releaser effect;
- signals modify the internal state of the receiver: primer effect.

This classification comprehends mechanisms, which are active in the process of evolution, determined by the special relations between organism and environment. This also causes their development during evolution as elementary constituents of animal behaviour.

If this is right, we have to expect differences between these signals related with the special class of effect. We have to ask, which are the parameters of signals, which affects kinesis, taxis, elasis, chronobiological alterations, releaser or primer effects. In this sense, we distinguish between affin signals, affecting approach, diffuge signals affecting withdrawal, and ambivalent signals affecting maintaining of a given distance. Their may be further universals of signals systems. The releasing stimuli of the ethologists will be mentioned here, also the directing stimuli. Are there general

features? Our knowledge is fragmentary and casuistic. Especially the releasing stimuli are species-specific and often very complex. The primer effect is also species-specific. In this context we also have to consider, that motivated communicative behaviour will be realized (if we generalize) in three 'fields of behaviour':

- the field of contact; the partner are able to establish physical contact, elements of adjusting and coordination are dominating in the interaction;
- the field of proximity; mutual identification has been performed, the interaction are orientated, signals secure the exchange of informations with respect to synchronisation, synlocalization and special forms of cooperation;
- the field of distance; this is the field of orientating behaviour, only special form of biocommunicative signals are able to establish an actual connection between the partners, reducing distance in time and space they can lead to the field of proximity.

In this context we also may expect special parameters of biocommunicative signals, adapted to the field of realization. We have found, that in rhythmic sequences the duration of intervals shows significant differences, if specialized to the field of contact, or proximity, or distance. Extremely short intervals we found in the field of contact. Thereby we have to consider, that in birds the ability of temporal dissolution is higher than in man.

Additionally we have to consider the ecological factors with respect the transmission of the signals; they determine not only the modality of the signals, but the qualitative properties also.

In this context, it is necessary to regard the distinction between r- and K-selection. It seems, that the two principles are also realized in the evolution of signals:

- r-selection with poor structured signals, produced in high quantity,
- I-selection with qualitative structured signals in limited entities.

Songs of birds seem to be ambivalent with this respect; this confirms their evolutionary multivalence, and perhaps all of the effects specified above may be included.

To evaluate the parameters, influenced by the general features, represented in this paper, we use the following treatments to analyze sequential signal processes:

- statistics of elements: determination of the duration of single units,
- statistics of intervals: determination of the duration of intervals between single units,
- statistics of periods: determination of the duration between identical phases of the sequence,
- analysis of the structure of sequences: Discrimination of types of signals and regularities in their sequential order, elaboration of rules, application of special metrics to characterize sequential structures, including cluster analysis, the theory of graphs and similar methods, as employed in structural linguistics.

ACOUSTICAL AND VISUAL MECHANISMS OF THE NATURAL
BEHAVIOUR OF TREE-HOLE NESTLINGS

S.N. Khayutin

Institute of Higher Nervous Activity and Neurophysiology of the
USSR Academy of Science, Moscow, USSR

The present study will concern the dynamics of formation of acoustic and visual mechanisms, that are basic for the early forms of behavior of pied flycatcher (*Ficedula hypoleuca*).

To study the age dynamics of the development of these mechanisms, we undertook the recording of evoked potentials (EP) from field L in the caudal neostriatum in 1.5-7.5 day old nestlings in response to the presentation of pure tones and species-specific signals and from Wulst of 2-9 day-old nestlings in response to light flashes. EP were obtained through chronically implanted silver electrodes. EP were recorded in correlation with the behavior, induced by the presented stimuli; behavior was evaluated judging by electromyographic activity of neck muscles. Nestlings were placed in the conditions, approximating the natural ones as much as possible.

When the nestlings behavior has been studied under the conditions of natural habitat was found that by the moment of hatching they had only one type of behavior formed, i.e. begging in response to specific acoustic stimulation. Till 5-6th days when their eyes opened this behavior - the rapid lifting of the head with upwardly outstretched neck, beak opening and vocalization - was elicited by the succession of stimuli: a tap of feet on the nest-box when the bird arrived, a rustle of the nest material caused by the bird jumping on the nest edge and a special "food call" emitted by the bird. Spectral characteristics of the components of "sonic complex of feeding" are presented in Fig. 1, A.

Since day 5 begging is elicited by a short-term luminosity change, produced by the adult, entering the nest-box through the hole. The only signal, adequate for begging elicitation in 5-9 day old nestlings was found to be a two-component (off-on) luminosity change of 1.5-2.0 log. units, lasting 100-200 ms. Simultaneously with eyes opening and the change of modality of the triggering afferentation of feeding behavior, nestlings start to display passive-defense reaction in response to alarm call emitted by the parents (Fig. 1, B). This call induces the cessation of movements and vocalizations (freezing) throughout the time of its action.

The sonographic analysis revealed that the signals, meaningful for feeding and defense behavior of nestlings, took up the frequency range of 0.1-7.0 kHz. During the recording of field L EPs response to pure tones within the studied frequency spectrum of different sound pressure level (SPL), three age groups of nestlings were discovered which differed in the range of frequencies effective for EP generation.

1.5-2.5 days old nestlings. EPs to monotonal stimulation were recorded only in response to frequencies from 0.1 to 4.0 kHz. EP consisted of three constant components: P_1 , N_1 and P_2 ; their latencies and amplitudes depended on the frequency of the signal and SPL. SPL required for the occurrence of a

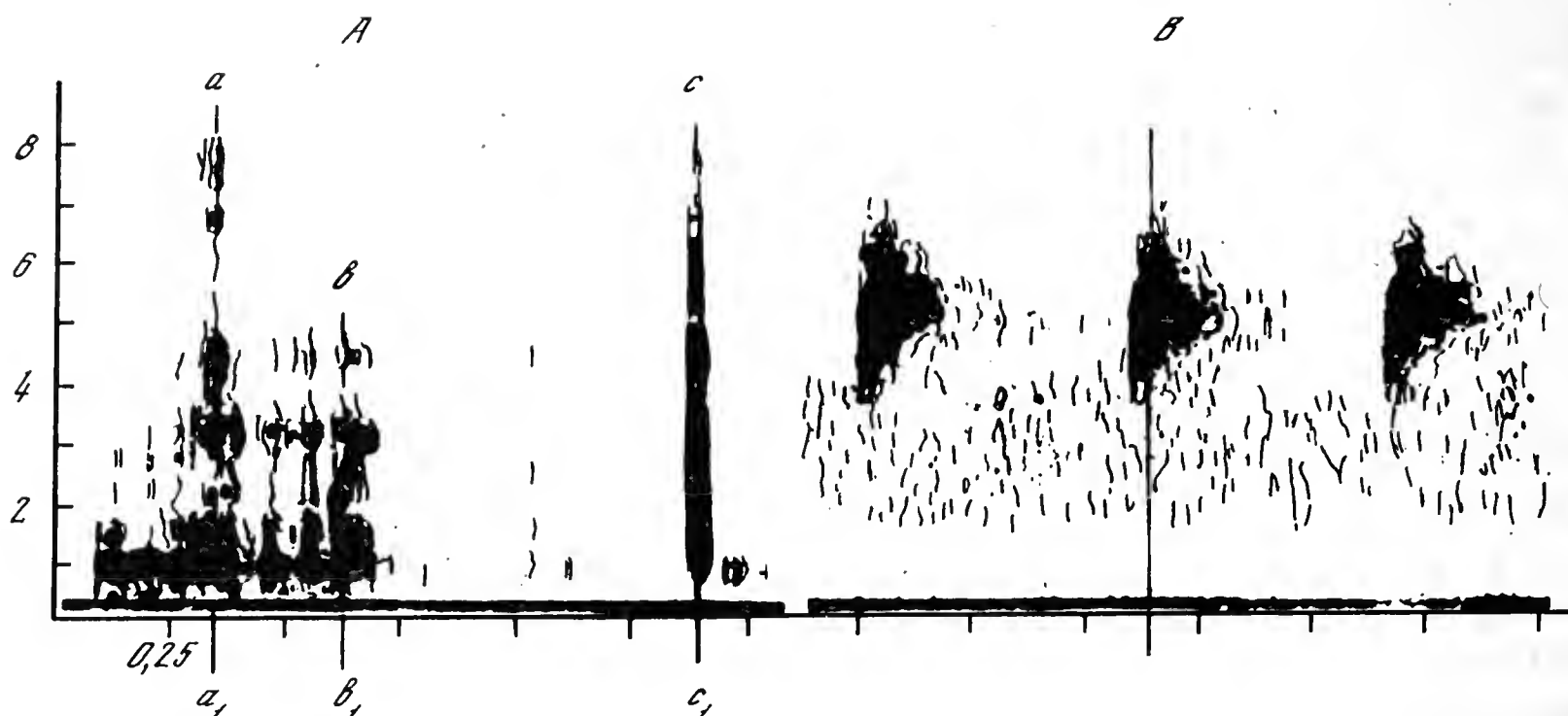


Fig. 1. Spectrograms of adult birds signals meaningfull for the behaviour of nestlings

A - sonic complex of feeding; a - feet tap on the nest-box; b - rustle of nest material; c - species-specific "food call". To the left of "a" - wing noises during the bird approach. B - species-specific alarm call. Abscissa - time, ms; ordinate - frequency, kHz

response had the minimal value in the frequency band of 0.5-2.5 kHz. EP in response to "food call" was characterized by the shortest latency, minimal SPL required for its (threshold) occurrence, by two additional components following P_2 and also by the maximal duration as compared with the responses to pure tones.

Considering that EPs the signals with frequency between 0.5 and 2.5 kHz occurred when the SPL was minimal and that the difference between the intensities effective to induce begging and EP was the smallest in the same range, we had to assume that the auditory perception of 1.5-2.5 days old nestlings was most completely formed in this range and that it was mostly significant with respect to its role in the behavior organization.

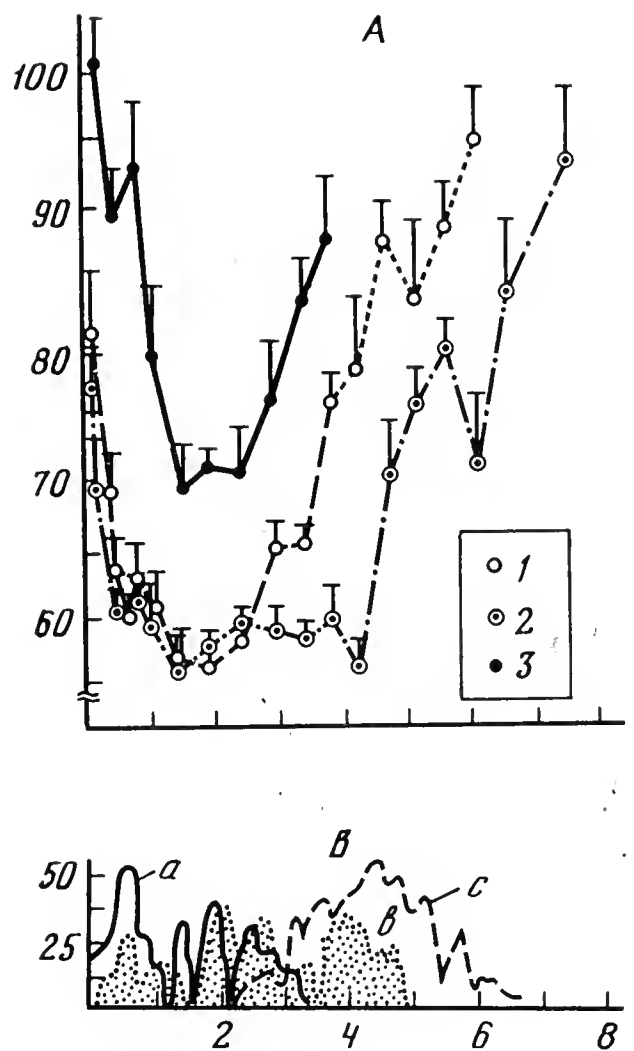
Nestlings 2.5-3.5 days old. The spectrum of perceived frequencies widened to 6.0 kHz. EPs to the tones of 4.5-6.0 kHz first appeared by the end of 3rd day of life. SPLs effective for the occurrence of the threshold EPs to these tones are presented in Fig. 2. Begging in response to the signals of such frequencies was never observed whatever intensities were used. EPs to threshold signals with the frequency from 0.1 to 4.0 kHz and to "food call" showed no detectable changes. All main EP characteristics in response to the frequencies inducing begging and the auditory-guided behavior itself did not change during this period.

Nestlings 4.5-7.5 days old. EPs were recorded in response to the stimulus frequency up to above 8 kHz. As compared to the preceding age groups the changes of auditory perception characteristics were mostly marked here. The

Fig. 2. Frequency-threshold curves of the auditory sensitivity of nestlings of different ages (A) related to the spectra of the signals, meaningful for their behaviour; energy sections of the signals, presented in Fig. 1 (along the lines a-a₁, b-b₁, c-c₁) (B)

A: 1 - thresholds of EP generation in response to the presentation of pure tones of various frequencies in the nestlings 1.5-2.5 day old and 2.5-3.5 day old (dashed line); 2 - in the nestlings 4-7.5 day old; 3 - begging thresholds in the nestlings 1.5-7.5 day old. Abscissa - frequency, kHz; ordinata - sound pressure level, dB.

B: a - geet tap; b - "food call"; c - alarm call. Abscissa - frequency, kHz; ordinate - relative sound pressure level, dB



SPL required for threshold EP generation decreased significantly in the range of 2.5-4.0 kHz and the other range of high sensitivity appeared - 4.5-5.0 kHz (Fig. 2). During this period no changes of any parameters of acoustic sensitivity in the range of 0.5-2.5 kHz were nevertheless observed. Minimal SPL in this range effective for EP generation did not differ from that defined for previous age groups. The pattern of feeding behavior as a whole also did not change though during this period the nestlings' eyes opened and so the modality of triggering afferentation of this behavior changed. Absolute values of SPL, effective throughout the whole frequency range for the organization of feeding behavior, stayed constant in the third period. As the thresholds for EPs generation in the range of 3.0-4.0 kHz decreased significantly, we can assume that the begging thresholds increase here (see Fig. 2).

The described facts show that the development of altricial nestlings' auditory system in the range of frequencies of the conspecific signals meaningful for their behavior is completed in the postembryonic period. The formation of auditory sensitivity in the range of 0.1-2.5 kHz (related to the feeding behavior) is completed during embryogenesis, while the sensitivity in the range of higher frequencies continues to establish during the first few days after hatching; the process is completed 2-3 days prior to the onset of the defense behavior, controlled by the sounds within this range.

As it may be inferred from Fig. 2, the spectral characteristics of the components of the "sonic complex of feeding" as a whole correspond to the range of frequencies, perceived by nestlings since the very first days of their life. Nevertheless, in spite of the general correspondence between the audition range and the spectrum of the signals, the narrow sensitivity peaks do not match

the dominant areas (energy maximums) of these signals, and so there is no strict correspondence in this case. All sounds of the complex have a "short-distance" effect as a recipient is situated very closely (3-10 cm) to the source of a sound which by the way spreads in a limited and closed space. Under such conditions the general correspondence of the auditory sensitivity to the spectrum of signals which are redundant in content, frequency and intensity are quite enough to serve the needs of the realization of a single behavior pattern.

In contrast to the complex of "food" signals an alarm call emitted by the parents from considerable distance from the nest reaches the recipient in a rather weakened form. So an auditory system of nestlings must possess other qualities to make use of it. Considering an important biological role of this signal (Khayutin et al., 1978) we may suppose that by the moment of organization of defence behavior nestlings must have a well matured mechanism for the selection of this call from the sonic environment created by the acoustic background of biotop as well as by their own vocalization. This mechanism has been found to be accelerated (two days prior to the occurrence of this behavior) formation of the narrow sensitivity peak around 4.5 kHz which exactly coincides with the dominant frequency of the signal. Additional factors increasing the security of perceiving this signal are its long duration and perhaps its rhythmic structure.

Thus two forms of acoustically-guided behavior substituting one another during early postembryonal ontogeny, i.e. feeding and defence behavior, are based on different principles of selecting them by the nestlings auditory system. And through these signal's spectra partially overlap they are nevertheless securely identified. On one hand defense behavior onset coincides with the cessation of acoustic signalization in the alimentary behavior and on the other - two days before the onset of defense behavior auditory sensitivity thresholds are rapidly decreased for the range of 3.0-4.0 kHz related to the feeding reaction. As the behavior thresholds of begging in this range remain unaltered an increasing gap is formed between the absolute thresholds of auditory sensitivity and behavioral thresholds of the feeding reaction. All this may prove the accelerated formation and the selection of one of the auditory sensitivity channels for the appearing form of behavior.

In the analyses of dynamics of formation of the visual mechanisms that are basic for feeding behavior since day 5 we took for an index the EPs recorded from wulst - the highest integrative center of avian visual system. The following facts were obtained. For the first time EPs in response to a luminosity change (2 log. units, 100-200 ms), imitating the natural visual stimulus of feeding behavior appeared in the 2.5 days old nestlings as a long-latency positive-negative deflection. The probability of EP occurrence and their parameters in 2.5-3.5 days old nestlings depended upon many additional factors. This juvenile EP was transformed into definitive one through a succession of stages common to all nestlings studied. The real duration of these stages, however, could vary in different youngs so the periods of EP formation presented below is somewhat schematized.

Age - 2.5 days - EPs occurred in the nestlings that were in the activated state: high feeding motivation level, movements in the nest, preening etc. EP occurred only in response to off-component of the flashes. Response latency (first positive peak latency) was 100 ± 8.4 ms.

Age - 2.5-3 days. Active nestlings responded with a long-latency low-amplitude complex to the off- and on-components of the signal.

Age 3 days. Active nestlings responded to off-component with high-amplitude rapidly developing EP; three main phases necessary for definitive EP could be distinguished in it.

Age 3-3.5 days. EP in the form of three-peak complex with the parameters and appearance like those of the definitive response occurred in response to on-component of the flash almost always.

Age - 3.5 days. EP consisting of three components was recorded in all cases. In the nestlings with high feeding motivation level the visually-guided form of feeding behavior was manifested for the first time. Begging occurred only sometimes and only in response to off-component of the flash, its latency being somewhat longer than the latency of evoked off-response.

Age - 4(4.5) - 9 days. EP in the form of a three-component complex looking much like the definitive potential was recorded in all cases in response to on-component of the flash and in 10% of instances - in response to off-component. Begging in the nestlings with high feeding motivation level coincided with the high-amplitude negative peak. Begging latency was 106.6 ± 17.7 ms.

Thus the formation and final arrangement of visual EP in the structure of the highest integrative level was completed between the 2.5 and 4th days of life. During 36 hours of postembryonal development the latency of response became 40 ms shorter and its amplitude (the high-amplitude first negative peak was taken for an index) increased twofold (Fig. 3). The most significant latency shortening took place in the interval between the first occurrence of EP and the onset of visually-guided feeding behavior while the amplitude growth continued also beyond this interval.

The study revealed that wulst EP are recorded for the first time on the 2.5th day of nestlings' life. Immediately after their appearance the responses occur not always, are unstable with fluctuating parameters. The probability of response manifestation and its markedness clearly depend on the level of general activation including feeding motivation level. EP in the form of low-amplitude long-latency complex are first observed in response to the off-component of the flash.

At the elder age when both responses to the same flash are recorded, off-component latency is shorter and matures earlier. Moreover, feeding behavior first occurs in relation to the off-component of the flash. All these facts make the supposition possible that general activating brain mechanisms play the most prominent role in the organization of early-ontogenetic response as well as the mechanisms of the specific (motivational) activation do. It is a

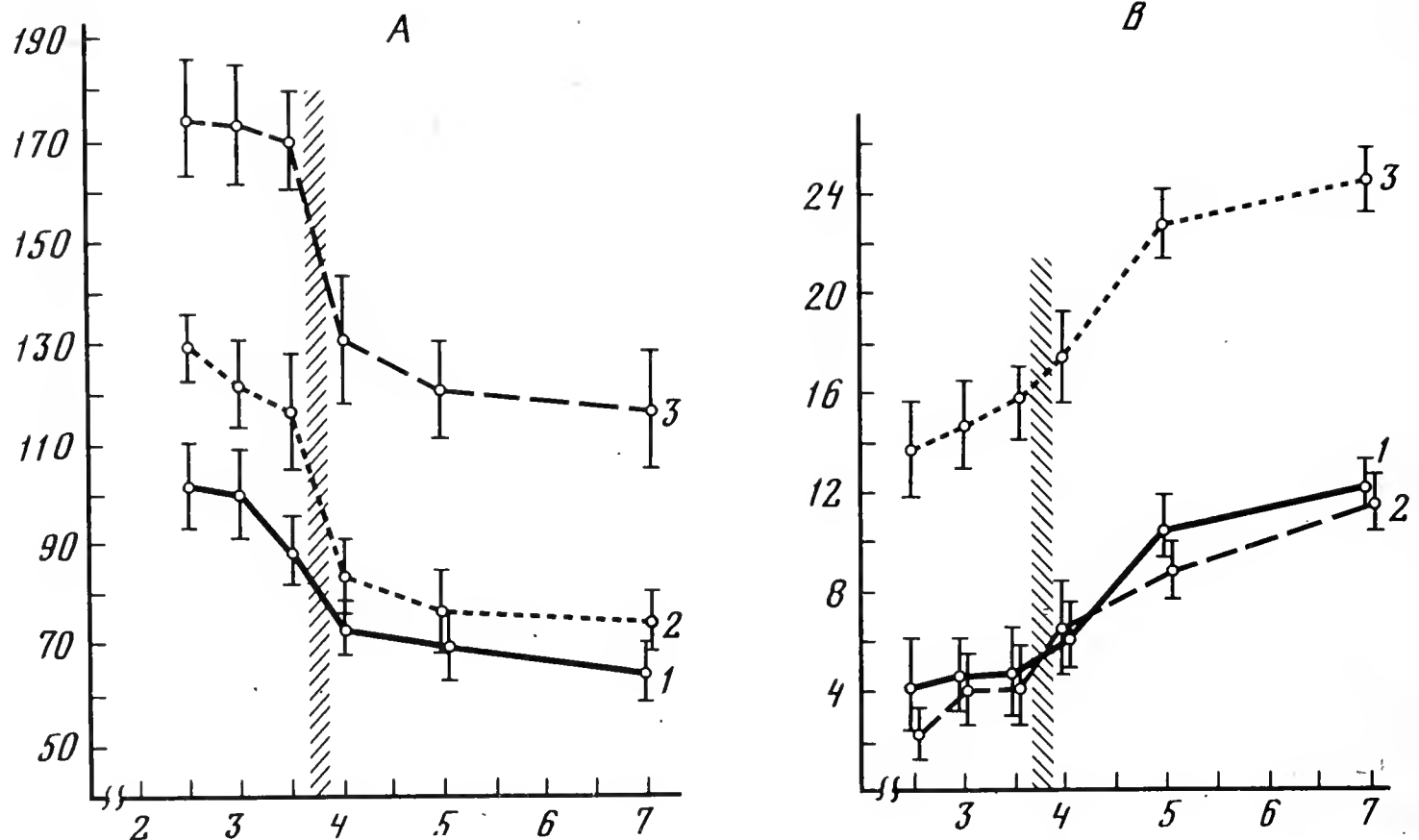


Fig. 3. Age dynamics of latency (A) and amplitude (B) of three visual EP phases: P₁ (1), N₁ (2) and P₂ (3). Darkened area - time of the appearance of visually guided feeding behaviour

Abscissa - age, days; ordinate: A - latency of the components, ms;
B - amplitude, μV

common fact that both systems may influence the activity of specific sensory structures in phasic as well as in tonic way.

Thus one of most important effects of early maturation of nonspecific and (motivational) specific activating mechanisms may appear to be their decisive influence on the rate of sensory mechanisms formation that in turn mediate species and individual adaptation to ecological factors. In this connection the aforementioned phenomenon may be understood, namely the accelerated maturation of the visual system and its involvement in the organization of goal-directed feeding behavior "ahead of schedule" in the nestlings that were developing in physically and socially enriched environment (Khayutin, Dmitrieva, 1981). This additional influence increased the level of general nonspecific activation which in turn initiated the early onset of functioning of specific visual mechanisms.

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Dieter Wallschläger

Sektion Biologie der Humboldt-Huversität, DDR-1040 Berlin,DDR

In contrast to the vocalization of other birds, woodpeckers have developed a special type of acoustical signals - so-called instrumental sounds. The most important form of communicating over a distance in many woodpeckers in the generation of drumming sounds. Drum signals are produced by rapid head and neck movements of the bird resulting in the bill striking a resonating substrate (usually wood). These sounds have a variety of functions discribed by Blume.(1977) as follows: species recognition, sex recognition, pair synchronization, indication of nest trees and territories.

In recent years we have attempted to decode the information content of these signals by analysing various temporal parameters of the instrumental sounds of nine European and some further North American woodpecker species and also to examine the relevance of this information to woodpecker behaviour. We have concentrated on the following parameres

- internal structure of drums (length and number of beats in a roll, time structure of the rolls - beat/beat intervals);
- time patterns of drumming sequences (roll/roll intervals);
- time patterns of mutual drumming sequences (roll/roll intervals from different individuals)(see Fig. 1).

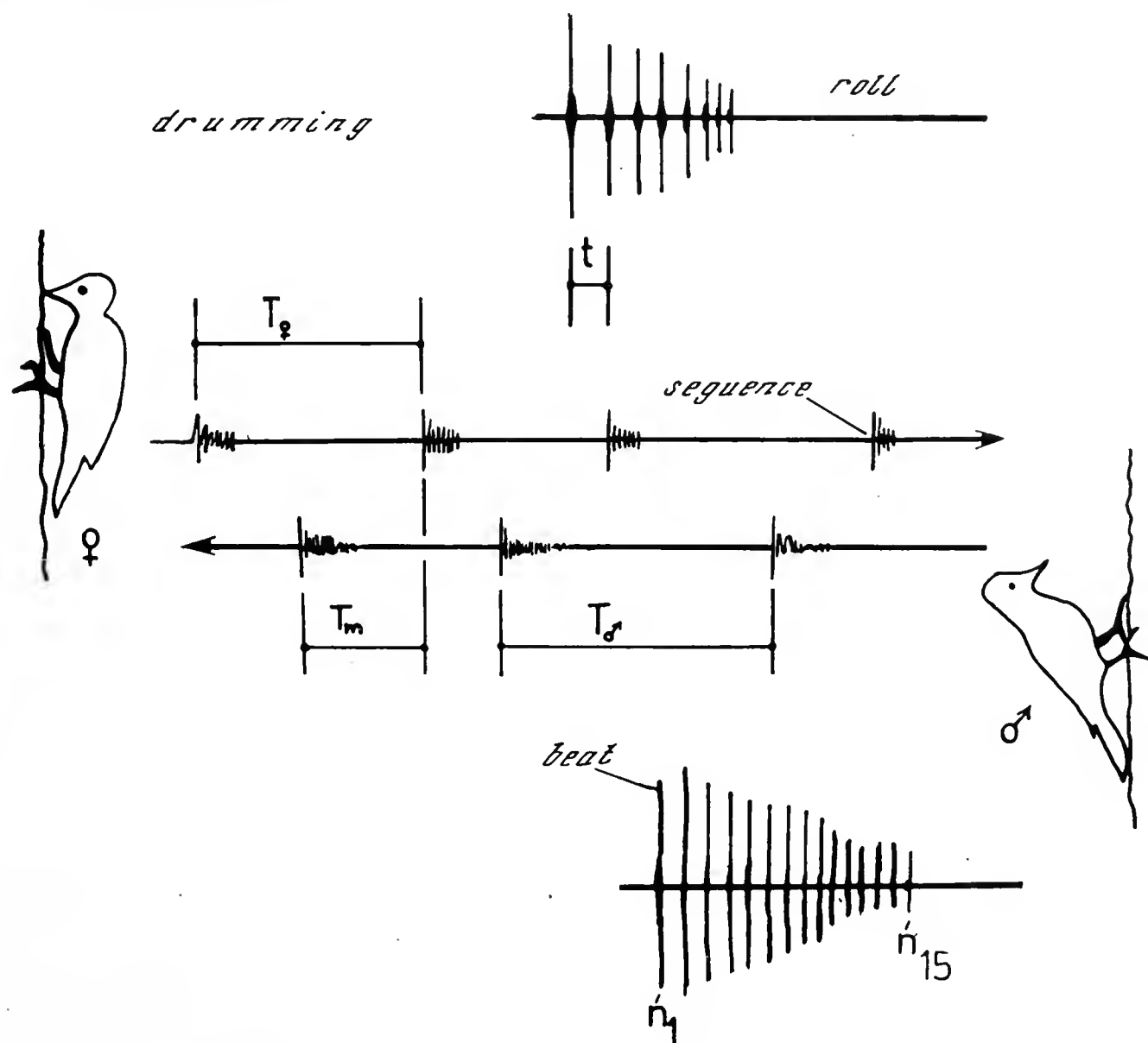


Fig. 1. The temporal parameters of the instrumental sounds of the woodpecker. t - beat/beat intervals, $T_{\text{♀}}$ and $T_{\text{♂}}$ - roll/roll intervals, T_m - roll/roll intervals from different individuals

Starting from the fact that birds attain a temporal resolution extending into the millisecond region we are able to show that woodpecker drumming constitutes a highly specialized information system. Individual types of information coded and transmitted by woodpeckers follow.

INTERSPECIFIC COMMUNICATION

The various woodpecker species compete for nests (hole trees) and food (see for instance Hogstad, 1958; Short, 1979). Drumming sounds may thus in themselves be seen as indicating the presence of a competitor. We are able to demonstrate interspecific reactions particularly in winter conditions using play-back experiments (Zabka, 1980). In particular *Dendrocopos minor* reacts to drumming sounds produced by *D. major* and *Dryocopus martius*. Interspecific reactions are also described by Winkler, Short (1978). The coincidence of certain information parameters may in spring lead to the formation of interspecific communication as is demonstrated by mutual drumming between *Dendrocopos major* and *minor* (see below).

INTER- AND INTRASPECIFIC COMMUNICATION

The most important objective of drumming is species recognition. This may in principle be indicated by both the length of the rolls and their internal temporal structure (Wallschläger, Zabka, 1979; Zabka, 1980). A statistical comparison of these parameters gives Fig. 2 (above-number of beats in the roll, below-length; non differing species are connected by lines). The time structure of rolls can be described mathematically by regression functions. The correlation coefficients obtained are highly significant (Fig. 3). Whereas linear regression functions dominate in the North American species *Dendrocopos pubescens*, *D. villosus*, *Dryocopus pileatus*, *Colaptes auratus* and *Sphyrapicus varius*, non-linear time structures of the beat/beat intervals are with the exception of the linear cases *Dendrocopos medius* (d), *D. minor* (e), *Picus canus* (h), *P. viridis* (i) typical of the European species *Dendrocopos major* (a), *D. syriacus* (b), *D. leucotos* (c) and *Dryocopus martius* (g). *Picoides tridactylus* is an intermediate case (f).

Play-back experiments using modified *D. major* rolls show that the first three beats of a roll suffice in evoking response reactions. The time structure correlates with ecological type in the case of the European species. Pronounced "peck" species ("Hackspechte") exhibit non-linear rolls, less pronounced species produce linear rolls. Of the North American species it appears that only the species *Picoides arcticus* exhibiting the highest level of pecking behaviour also produces speedup drumming. Since this form of drumming has evolved independently in different genera it may be assumed that it was generated by ecological factors leading to corresponding morphological adaptations. This view is supported by computer simulations using morphological parameters.

Besides the structure of individual rolls the roll sequences may also be

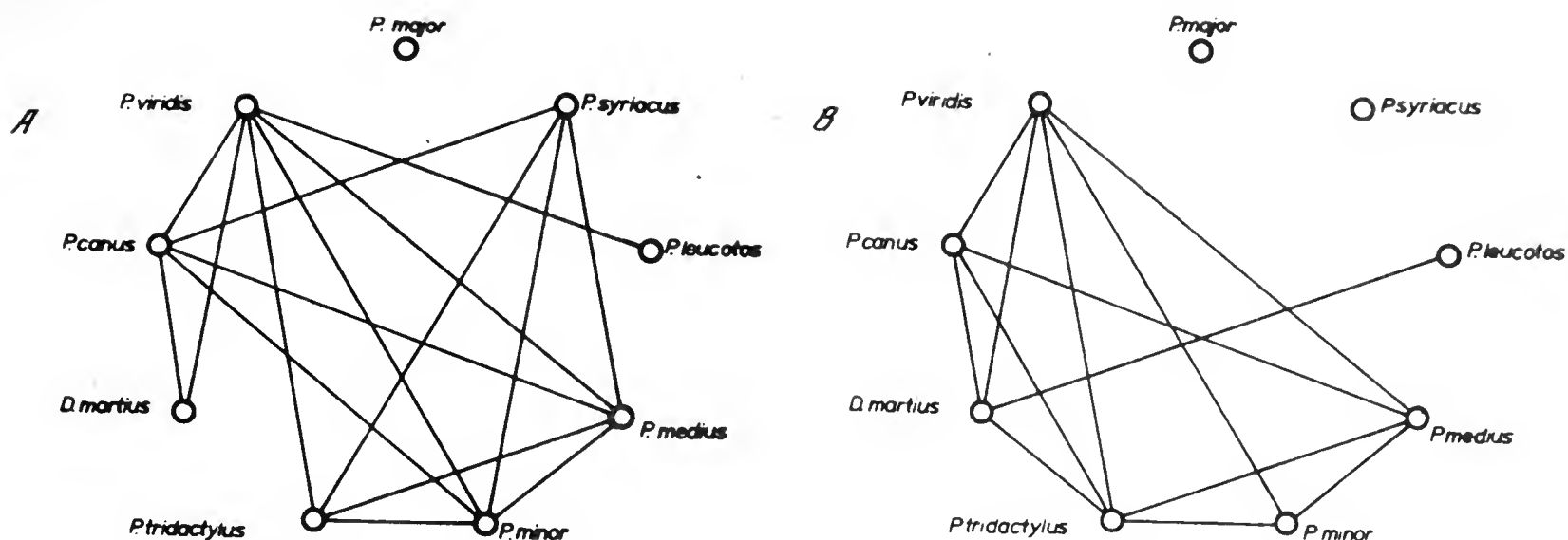


Fig. 2. A statistical comparison of beats in the rolls (A) and the length of rolls (B)

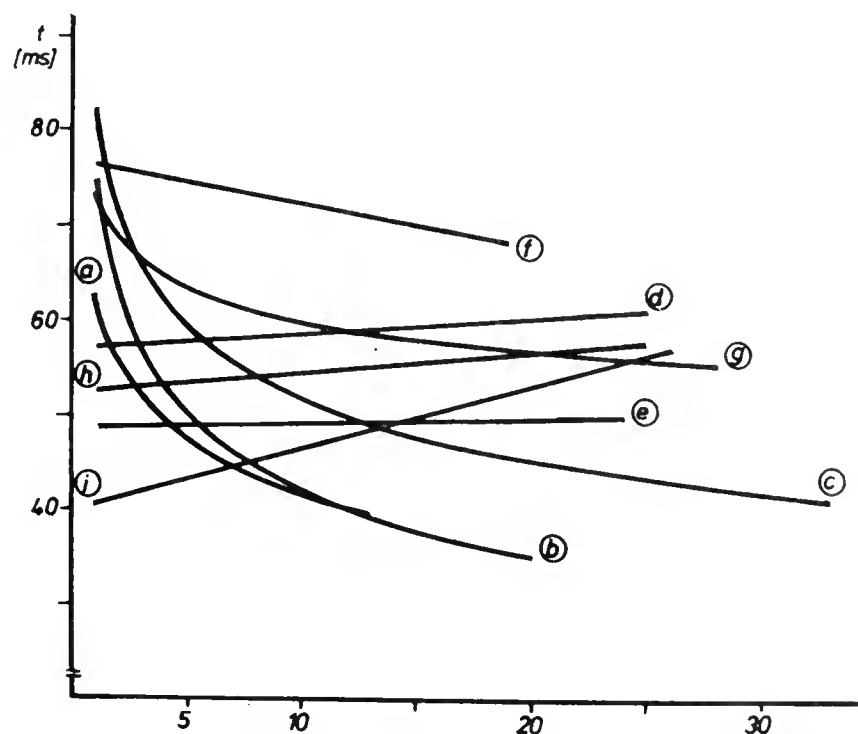


Fig. 3. The correlation coefficients of the time structure of rolls

used in species coding. Whereas intervals between rolls exhibit considerable variations in the case of D. major ($t_{\sigma} = 12.67$ sec, $V = 43.4\%$, $n = 7$; $t_{\phi} = 7.62$ sec, $V = 45.5\%$, $n = 5$), they are highly constant in D. minor ($t_{\sigma} = 5.81$ sec, $V = 23.1\%$, $n = 6$). D. minor preferred dummies in play-back experiments with intervals of 5 sec, D. major responded to arbitrary intervals up to 20 sec.

INTRASPECIFIC COMMUNICATION

Individual and seasonal variations of the duration of rolls are apparent in some species. In particular it is known in the case of some Dendrocopos species that females produce shorter rolls than the males (Blume, 1977; Winkler, Short, 1978). We have studied this phenomenon in the case of D. major over a number of years. The following results were obtained (Fig. 4): As a rule females commence drumming earlier than males. Very long rolls (up to 16 beats) as well as short rolls are produced in January. The length of the rolls

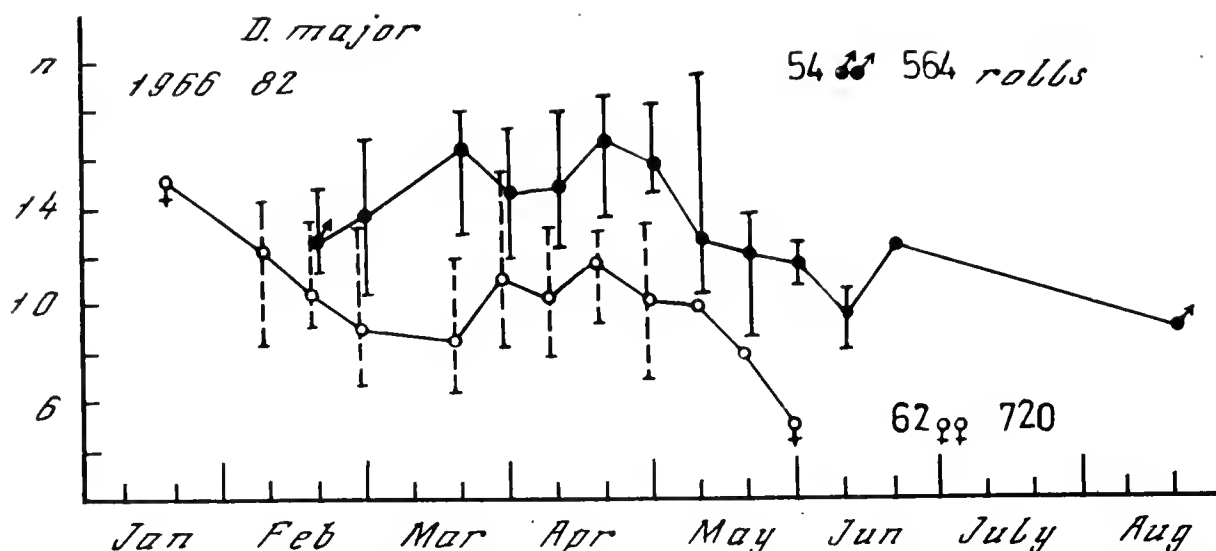


Fig. 4. Seasonal variations of the rolls' length in males and females of the Dendrocopos major

decreases in the course of winter and spring ($n = 14.17 - 0.42$ decade of the year, $p < 0.01$). Males do not start drumming until the latter half of February. Their rolls contain more beats and increase in length until the end of March. The rolls of males and females then exhibit the greatest differences (on average 9 beats). At this time of pair formation the sex-specific character of drumming is very pronounced. Male rolls attain a second maximum of the number of beats prior to egg-laying at the end of April. The difference between male and the as before longer female rolls is reduced to 5.2 beats. At this stage drumming obviously contributes to pair synchronization and stimulation of breeding. As a rule females cease drumming at the onset of breeding. Males continue drumming during and after breeding, their rolls are however considerably reduced (economic of energy ?). A similar mechanism for the Seasonal variability of roll length was described by Tilgner (1976) for the case of Dryocopus martius. Using our material we could only demonstrate the second phase (decrease of roll length - $n = 37.86 - 0.78$ decade, $p < 0.05$). The late onset of drumming in our observation area (North of the GDR) may result from low population densities implying that drumming mainly serves in pair synchronization.

The different number of beats is particularly apparent in mutual drumming between males and females, which may often be heard in March and April. This is preceded by mutual drumming between individuals of the same sex which is involved in territory marking and defence. In all of the ten long mutual drumming examined the beat number samples varied significantly ($p < 0.01$ and mostly 0.001). The number of beats is thus in certain limits an individual characteristic (at least in the case of neighbours engaging in mutual drumming) and in particular a sex characteristic (Fig. 5). Similar circumstances are encountered in the case of D. minor. Neighbouring woodpeckers produce rolls with greatly differing beat numbers.

A further characteristic involved in sex recognition is the distance between the first two beats in the case of D. major. This is usually longer than 65 msec in females (a) and only about 60 msec in males (b) (Fig. 6). D. minor also exhibits a relation between the first interval of a roll and roll length. Since in this species males and females can both vary their beat numbers this is only considered here as an individual characteristic. One can assume that

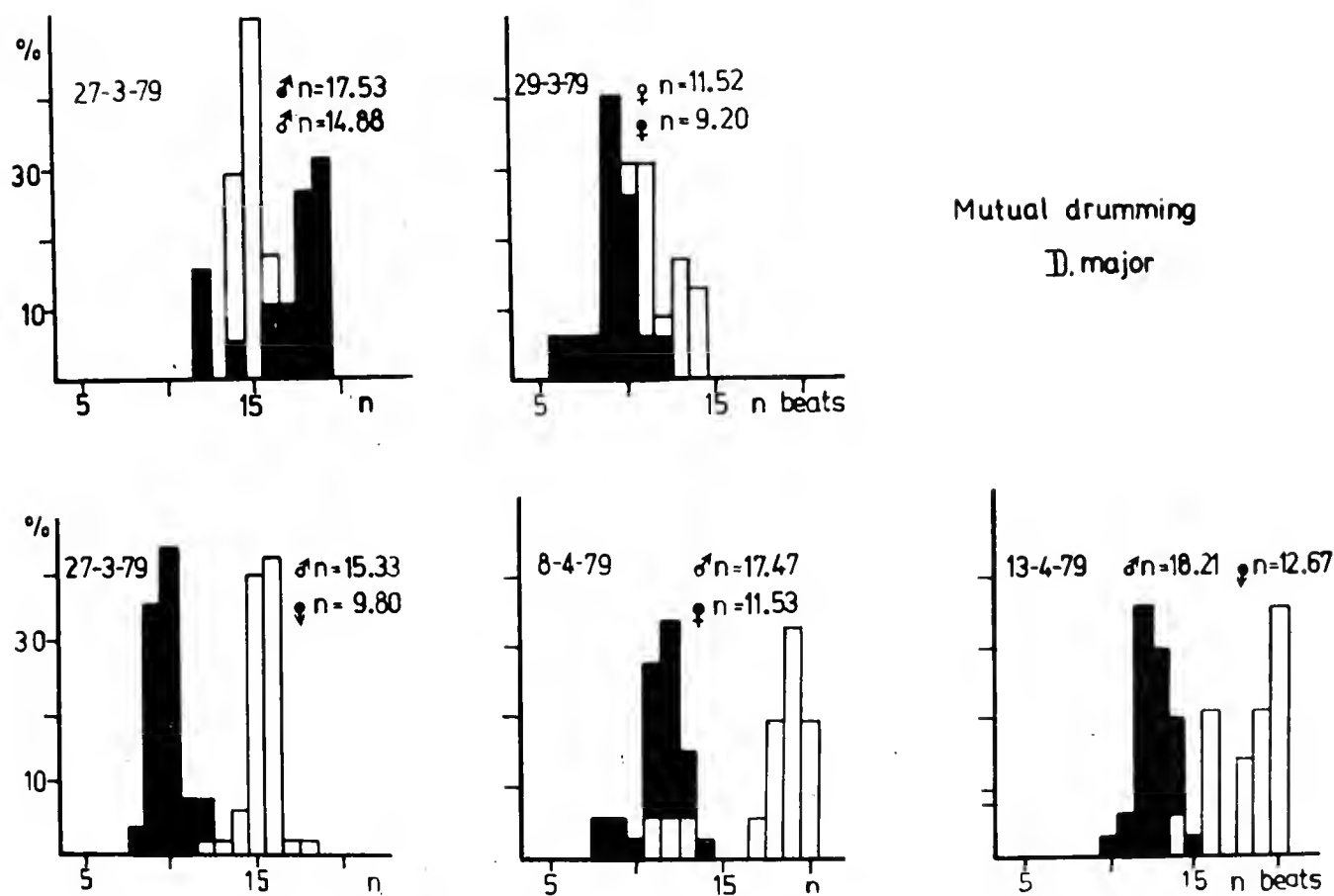


Fig. 5. Mutual drumming of the *Dendrocopos major*

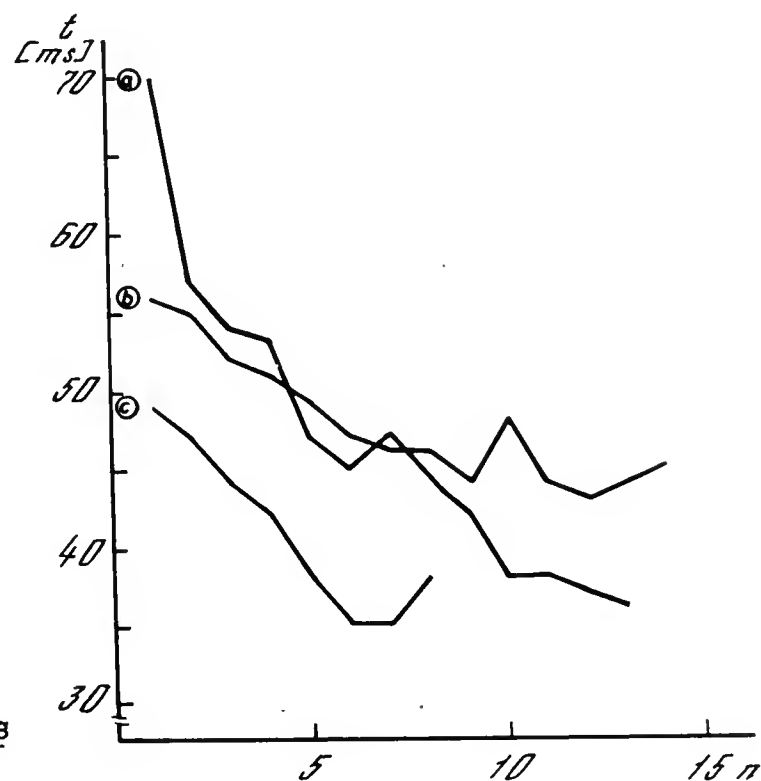


Fig. 6.

The distances between beats in the rolls in the *Dendrocopos major*

this relation between first beat interval and beat number as demonstrated in two species constitutes a basic coding mechanism for sex or/and individual identification in woodpeckers.

Mutual drumming is a complicated form of supraindividual vocalization which mainly serves as a mean of pair synchronization. It is apparently most highly developed in the species *Dendrocopos major*, *syriacus*, *tridactylus*, *leucotos* and *minor*. Analysis of the time structure of *D. major* mutual drumming shows that the intervals between individual rolls of male and female tend to be similar and that in comparison to birds drumming individually the variation coefficients are greatly reduced. As opposed to values of around 45% synchronization can give values under 20% (on average about 25%). It appears

field observations and provoked mutual drumming intervals of mostly between 11 and 14 sec were registered. The responding woodpeckers adopt the displayed rhythm after only a few rolls. Dendrocops minor only responds in exceptional cases to dummies which differ from the species-specific rhythm of about 5 sec. Mutual drumming between D.major and minor is thus exceptional. As a rule in such a case D.major responds to fast D.minor roll sequences.

In exceptional circumstances D.major drumming rolls with abnormal structure may be heard (Fig. 6c). Such mostly uneven roll are produced by young birds during territory claiming in summer. The emotional state also influences the time structure. If for instance a male lands near to a drumming female the roll structure changes immediately. In such a case emotional stress obviously causes a temporary disturbance of the central nervous control mechanism.

The results on instrumental sound communication given here only constitute part of our investigations. Many questions could only be discussed in one or two species. Woodpeckers have in the course of their evolution developed a unique system of communication. This system is mainly based on time patterns.

SUMMARY

Instrumental sounds play a fundamental role in acoustic communication in woodpeckers. Drumming guarantees different functions of behaviour. The analysis of several parameters of drumming rolls (roll length, internal time structure, roll sequences, mutual drumming) revealed that all European woodpecker species possess drumming rolls with specific time structure which most likely are genetically determined.

1. Interspecific communication - foraging and nest tree competitor drumming: especially in the winter season;
2. Inter- and intraspecific communication - species recognition (internal time structure of drums, time patterns of drumming sequences);
3. Intraspecific communication - sex recognition (roll length and its seasonal variation at least in Dendrocopus major, D.syriacus and Picoides tridactylus);
4. Pair recognition and synchronisation (mutual drumming at least in D.major, D.syriacus, D.minor, P.tridactylus, Dryocopus martius);
5. Individual recognition (roll length);
6. Expression of emotional state (sudden change of internal time structure of drums).

Drumming of Woodpeckers is a high invariable communication system, which chiefly is based on time patterns.

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THE VOICE AND HEARING OF BIRDS IN ONTOGENY

T.B. Golubeva, A.V. Tikhonov

Department of Vertebrate Zoology, Moscow State University, Moscow, USSR

It is well known that in the life of birds sound communication is of great importance, and it is only natural that the allround study of acoustic communication leads to the investigation of formation of not only the voice but also the hearing in ontogeny. The indissolubility of these two processes can well be traced in the works by G. Gottlieb (1971), V.D. Ilyichev (1972, 1975) and some others.

We used the method of registration of cochlear microphonic component (CM) to study the development of hearing. CM represents the total response to the acoustical stimulation of the sensitive hair cells of the basilar pappila. The notion on the development of hearing was based upon the analysis of the threshold and frequency-amplitude characteristics of CM in embryos and nestlings of different age. The morphological characteristics of maturation of the basilar pappila were obtained by the methods of light histology and scanning electron microscopy. Comprehensive investigations on the development of hearing sensitivity have been performed for six species of birds with different types of ontogeny. The domestic Peking duck (Anas platyrhynchos domestica) was used as a representative of precocious birds, and the common and herring gulls (Larus canus and L. argentatus) as well as the Arctic tern (Sterna paradisea) represented semiprecocious ones. Among the birds presenting nudiformes we studied the jackdaw (Coleus monedula) and the long-eared owl (Asio otus).

The study of regularities governing the development of voice in the early ontogeny was carried out on the representatives of 12 orders of birds including over 100 species of precocious, semiprecocious and nudiformes. These investigations were conducted in conditions of artificial incubation of eggs as well as in natural conditions when the eggs are brooded by the parents.

According to our data the faculty of hearing is acquired by precocious at the beginning of the second half of the incubative period. It agrees with the data on the evolvement of hearing in birds given in the literature (Vanzulli, Garcia-Austt, 1963; Konishi, 1973; Saunders et al., 1973). These data refer also to the precocious birds: the embryos of hens and ducks. No studies have ever been made on the development of hearing in semiprecocious birds. According to our data their CM can be detected since the beginning of the last third part of the incubative period, and in the nudiformes - since the moment of their hatching or on the eve of it. The emergence of hearing sensibility precedes the origination of vocalization in all the studied species.

Fig. 1 presents the changes in the average levels of CM thresholds over a period of the whole process of development of hearing in three species of birds: the Peking duck, the common gull and the jackdaw. On these graphs one can trace both the general regularities and the specific features of the process. The prenatal and postnatal days of ontogeny are plotted on the abscissa, and the levels of CM thresholds in dB with respect to the regular level ($2 \times 10^{-5} \text{ N/m}^2$) - on the coordinate axis. In the beginning all birds display

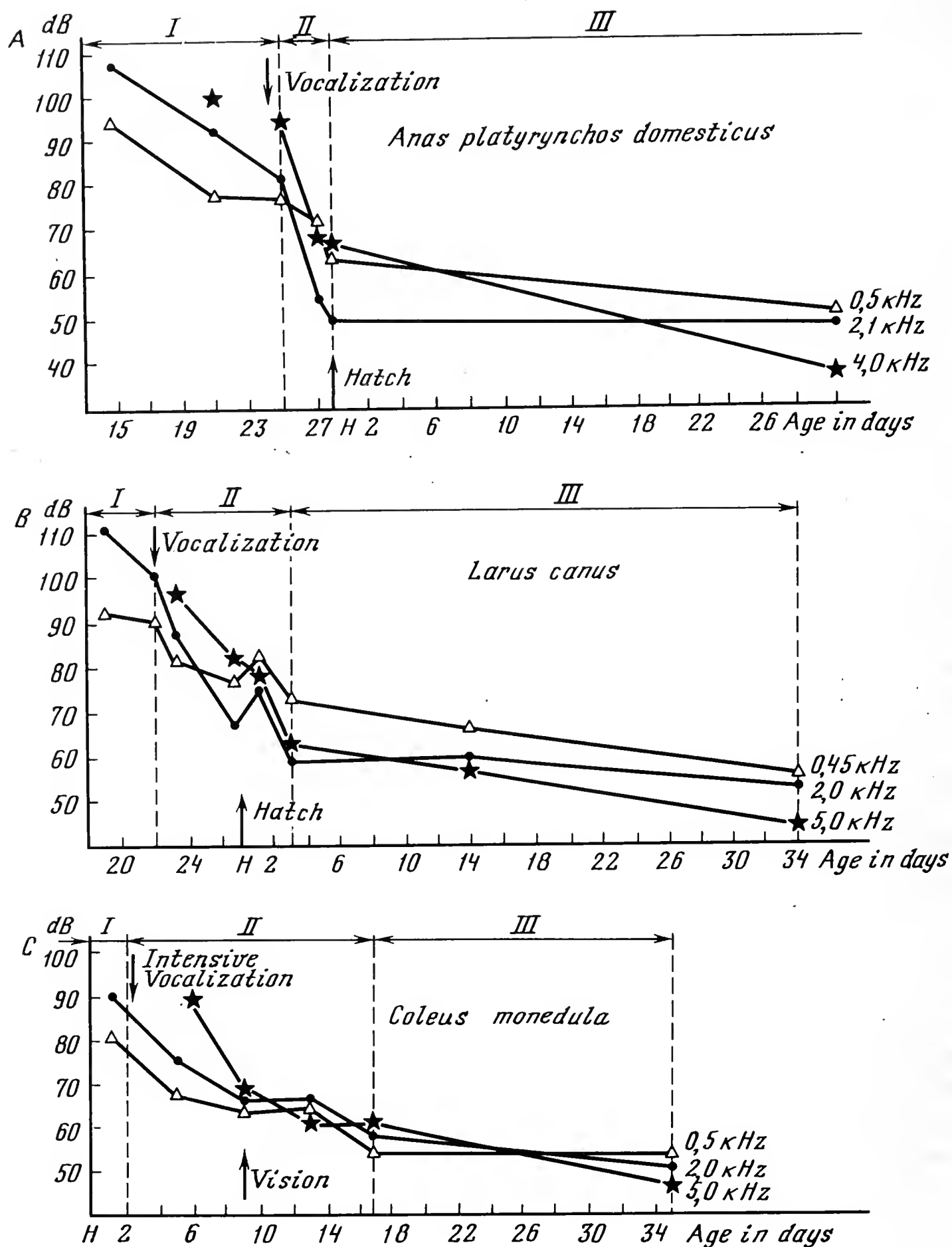


Fig. 1. The changes in the average levels of CM thresholds during ontogenesis in precocious (A), semiprecocious (B) and nudiformes (C) birds

sensibility to the low frequencies in the range up to 2 kHz. When the birds are growing the range of their perceptible frequencies is expanding, and their CM thresholds which prove to be very high in the initial stage are lowered. By the time when the nestling is capable of flying and begins an independent life its hearing characteristic assumes the form typical of adult birds.

As it can be seen from Fig. 1 the rate of lowering the CM thresholds in

different periods of hearing development is not the same. We have revealed three stages of development in the hearing sensibility of all the studied species.

The first, i.e. the initial stage, can be characterized by high CM thresholds and a relatively moderate rate in the development of sensibility. The initial stage is the longest in precocious, and it is very short in nudiformes. The second stage is distinguished by a quick lowering of the levels of CM thresholds and an intensive assimilation of the high-frequency range. In all species the onset of the second intensive stage coincides with the advent of an intensive inherent vocalization (marked with an arrow). This is just the moment when the hatching bird begins to produce an ever growing number of acoustic signals: according to our data from 5 to 8 times more than before it. Then there comes a period of acoustic communication between the brood-hen and the embryos as well as among the embryos themselves. The stage of intensive development is the shortest in precocious birds. In the duck it lasts from the 24th day of incubation to the moment of hatching, i.e. about three days. In the gulls this stage lasts for about 8 days and includes the first days after the hatching. In nudiformes the intensive stage is the longest: in the jackdaw it takes 14 days of the postnatal ontogeny and in the long-eared owl - about three weeks.

It follows that each type of ontogeny affects the duration of stages in the development of hearing.

In the process of hatching one can detect a certain delay in the development of hearing sensibility in precocious and semiprecocious birds; in nudiformes the same delay is associated with the recovery of their sight.

In the course of the last third stage the hearing sensibility is improving over the whole range of perceptible frequencies, but the rate of this process is substantially decreasing. However, this is just the time when the CM amplitude is intensively growing and the formation of hearing sensibility to high frequencies typical of adult birds is completed. We believe that in chicks and nestlings these processes must be connected with formation of their chemical thermoregulation and with the growth of middle ear's structures.

In representatives of different systematic groups the terms of the onset of vocalization vary a great deal, and in this case it is easy to note an early emergence of vocalization in Rheiformes, Procellariiformes, Rallidae, Laridae and Alcidae (Table 1). The first acoustic signals in embryos are registered even before the beak goes out into the egg's air space, i.e. during the first stage. The origination of these signals is associated with the "irregular" respiration of embryos which is realized at the expense of the air bubbles in the amnion cavity. The first pippings of embryos are single-sounding. They are of low intensity and separated by extended time intervals (Fig. 2).

The analysis of the spectro-time structure of the first pippings of embryos shows that in all species irrespective of their systematic grouping and the type of individual development the initial modulation of frequency has an almost bell-shaped form. Our experiments involving the bilateral denervation of syrinx in embryos at the moment of manifestation of vocalization showed that

T a b l e 1. Onset of the vocalization in bird's embryos

I - systematic groups of birds; II - Stages of embryos development in % from the total incubation

| I | II | I | II |
|-------------------|-------|--------------|-------|
| Rheiformes | 84-85 | Rallidae | 86-91 |
| Gaviiformes | 92-93 | Charadrii | 89-92 |
| Podicipitiformes | 92-93 | Laridae | 85-94 |
| Procellariiformes | 85-88 | Alcidae | 85-92 |
| Pelecaniformes | 92-94 | Strigiformes | 93-94 |
| Ciconiiformes | 92-94 | Motacillidae | 97-98 |
| Anseriformes | 88-90 | Sylviidae | 97-98 |
| Falconidae | 93-94 | Corvidae | 94-95 |
| Galliformes | 93-94 | | |

the mechanism of origination of these first signals does not require any nervous control over the vocal musculature of the inferior larynx. Stabilization of nervous control over the tension of tympanic membranes is realized in ontogeny stage by stage. The primitive (passive) type of sound-production performed without an adequate nervous control of the syringeal musculature is represented in the early stages of ontogeny, and it is retained in adult birds only in certain most ancient calls, for example, in distress calls. This suggests that as the early stages of ontogeny the vocalization in birds in its development so to speak reiterates or, according to the definition of A.N. Severtsov (1939), recapitulates the stages and mechanisms of sound-production inherent in the evolution of more ancient, ancestral forms.

Next to the pippings the embryos begin to produce occasional clicks originated owing to the mobility of the cartilaginous superior larynx (McCoshen, Thompson, 1968) and accompanying each respiratory act of the embryo.

Once the embryo's beak works into the air space its sound projection is drastically intensified. This is just the moment when the stage of intensive hearing sensibility sets in. Since the time when the egg-shell is pecked through and the embryos begin to breathe inhaling the atmospheric air, the acoustic signals acquire a rhythmic organization forming the series made up of several impulses. The occasional clicks are getting regular. Various forms of frequency modulation differing from the bell-shaped form can be detected in birds having a complex structure of their larynx. A distinct situational differentiation in signals becomes most evident. Right after the egg-shell is pecked through in precocious and semiprecocious birds one can detect the distress calls replacing the pippings. Some time later you can hear the pleasure calls, then the feeding calls and so on (Tikhonov, 1980a). Prior to hatching the precocious and semiprecocious birds dispose of almost the entire set of signals inherent in the nestlings on the first days after the hatching. However, no alarm calls have ever been registered in embryos (Ilyichev, Tikhonov, 1979; Tikhonov, Fokin, 1981, 1982; Tikhonov, 1980a).

When the egg-shell is pecked through, nudiformes dispose only of distress calls of low intensity, and the rhythm of these calls is stabilized just before the distress calls assume the role of feeding calls and, when the little ones are sated or sleeping, these calls are substituted by the harmonic plea-

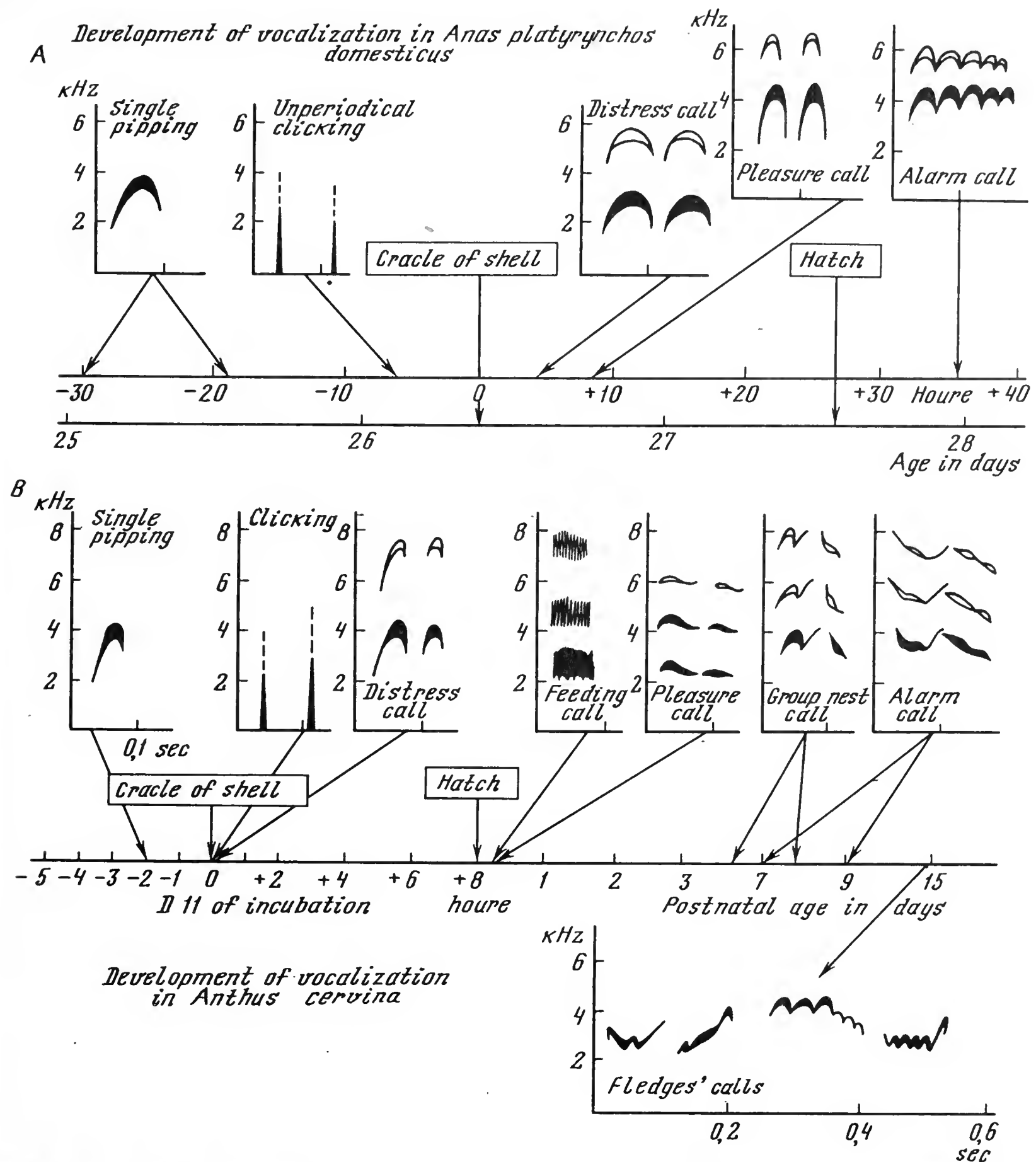


Fig. 2. Development of vocalization in precocious (A) and nudiformes (B) birds

sure calls. Further differentiation of acoustic signals in nudiformes birds is accomplished during the postnatal ontogeny after the recovery of sight. Then come into being a group call of nudiformes, alarm calls, fledges' calls and so on (Fig. 2,B).

It follows that heterochronism in the development of acoustic signals represents the most important feature of ontogeny in the birds' voice. The alarm calls and the protective behavior acquire the adequate form only after the recovery of sight in the course of direct contacts with the adult birds, in the families. In the absence of such contacts the specialized calls of alarm caused by some approaching terrestrial or feathered predators are ma-

nifested much later. For example, in Galliformes and Anseriformes they are detected on the 5th-12th days, and moreover these calls do not correspond to the respective situations (Tikhonov, 1980b). It is obvious that in the process of formation of the nestlings' defensive functional system an important role is played by the "environmental training". (Manteifel, 1977), whereas the formation of the feeding functional system acquires a more definite character.

In the early ontogeny the vocal set of birds' sounds is determined not only by the type of ontogeny but first of all by the species ecological peculiarities. Two clearly defined classes of signals of distant communication are inherent in the nestlings of colonial species of Laridae making their nests on the ground (Larus argentatus and L.canus, Sterna paradisea and S.hirundo): the orienting and distress calls providing a means of individual discrimination and the appropriate acoustic orientation. The structure of the brood is retained due to these signals. We believe that this peculiar ecological requirement is just the factor determining the registered strict correlation in the spectra of acoustic signals and the regions of maximal sensitivity of gulls and terns in the early ontogeny (Golubeva, 1978, 1980, 1982). No specialized orienting signals can be detected in kittiwakes: nesting on the rocks excludes any possibility to leave one nest for another and there is no need in forming strictly definite individual distinctions. The orienting signals are inherent in the nestlings of Alcidae, such as Uria aalge and U.lomvia having colonial nesting sites, but they are not detected in Gavia or Cephus grylle making solitary nests, neither are they produced by Fratercula arctica forming colonies, but nesting in holes.

The analysis of signals of all types reveals certain age changes in their respective integral spectra. In the course of aging the main energy-producing components of the spectra are shifting to still higher and higher frequencies. We could observe that in this process the spectra of the inherent signals always coincided with the main region of hearing maximal sensitivity. Following the movement of the main energy-producing component towards the higher frequencies, the region of maximal sensitivity is also shifting so that the correlation between the region of hearing maximal sensitivity and the spectra of the inherent signals may be preserved at all times (Fig. 3). In the second stage of the development of hearing sensibility this correlation can be traced most distinctly. Then it is leveled, and the movement of the main energy-producing components of the spectra of signals proceeds so to speak in the opposite direction: when the spectra of signals exhibit and overall expansion, they are shifting to the lower frequencies.

Whereas the rate of lowering the CM thresholds in all the studied species is approximately the same during the first and the third stages, the second stage is distinctly more pronounced due to the ecological conditioning in raising the hearing sensibility. Firstly, the average rates of lowering the CM thresholds are the highest in precocious and lowest in nudiformes. Secondly, the highest rate can be observed at the frequencies corresponding to the main energy-producing components in the spectra of signals inherent in embryos and nestlings. In the duck the rate of raising the sensibility at these frequencies amounts to 14 dB per day. As to the nestlings of a jackdaw, in which the trophic signal can be associated with certain noisy sounds, the

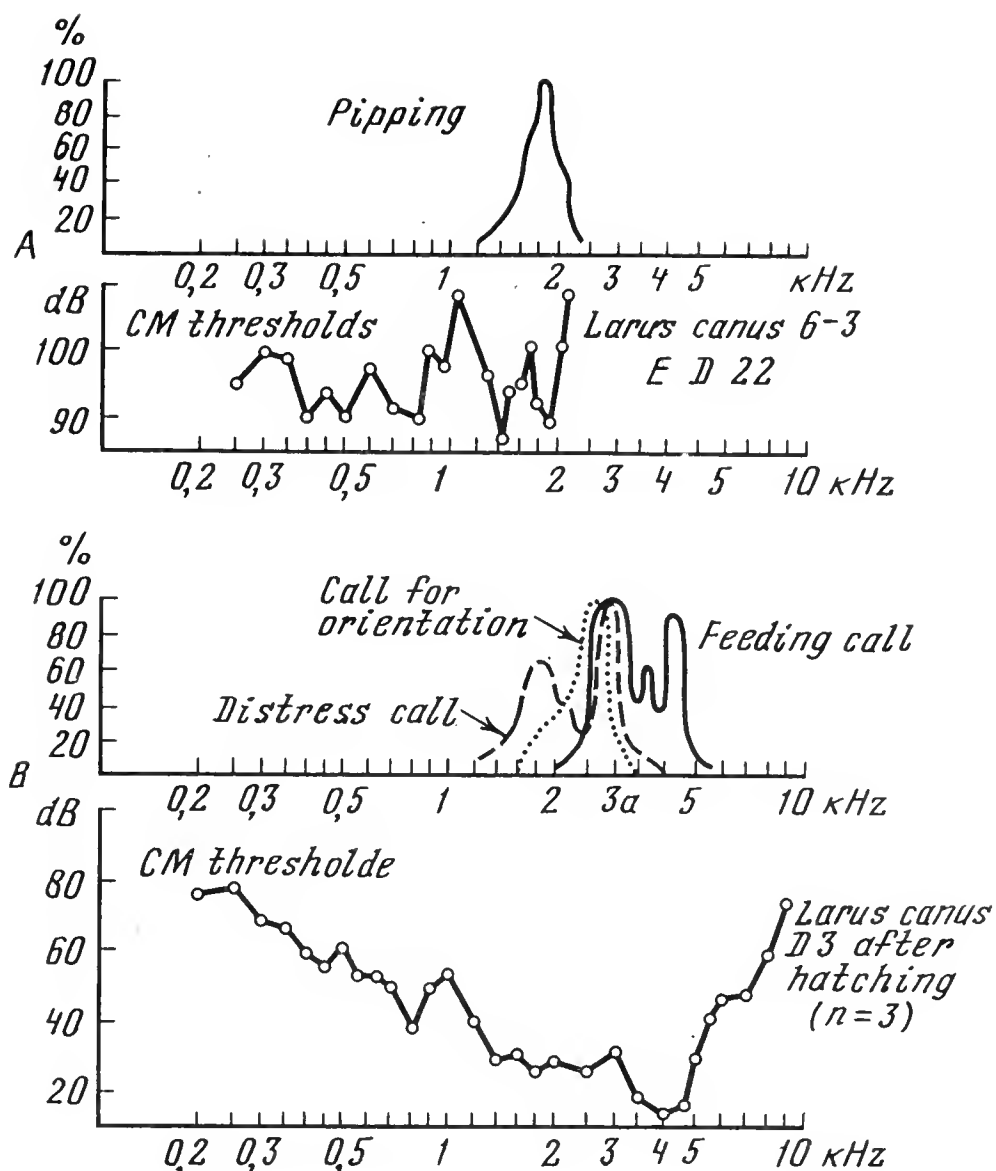


Fig. 3.

The correlation between the integral spectra of embryos' and chicks' calls (%) and their CM thresholds (dB)

A - *Larus canus* embryo D 22, B - *Larus canus* 3 days old chicks

rate of lowering their thresholds is comparatively uniform over the whole range of frequencies.

It follows that during the second stage the species regularities, governing the formation of vocalization, determine the character of development of hearing sensibility.

The acoustic information perceived by the embryos and nestlings is not only an important factor regulating the behavior of an individual in the community but also a factor of physiological development of the organism. The acoustic communication between the embryos as well as their communication with the hatching bird accelerates the embryonic development and promotes synchronization in the hatching of squabs. M. Vince (1964) was the first to show that in precocious birds mutual stimulation of embryos based on the "clicking" sounds plays an important role in this process. We have found out that the nandu, Galliformes and Anseriformes display the greatest ability to synchronization in hatching. In the nandu the time required for the hatching of all the squabs in a clutch ranges from 30 to 90 minutes, though the total number of its eggs amounts to 16 and the male starts hatching as soon as the first egg is laid out. Among Galliformes the maximum synchronization has been detected in the hazel hen: its time of hatching is 20-30 minutes and there are up to 12 eggs in one clutch. In the garganey teal the time of hatching for all the clutch of 10-12 eggs amounts to 60-75 minutes.

It has been confirmed by the experiments that the embryos of precocious birds are capable of adapting themselves to the rhythm of emission of clicks exceeding their own, i.e. they can intensify their own respiration. In this way the embryos with retarded development adapt themselves to the rate of evo-

lution characteristic of the eldest embryo (the leader). This process leads to intensification of not only the pulmonary respiration but also the metabolism as a whole. Among other things it accelerates the development of the trophic functional system, contributes to the absorption of the remaining yolk into the cavity of the body and leads to a concordant termination in the development of embryonic stages. In our opinion the retarded development of the embryo, incubated in a group of considerably younger ones, is caused by the heat emission regularities rather than by the effect of a low rhythm of clicks produced by the embryos of the principal group (as is suggested by Vince, 1968, 1973). When the number of younger embryos proves to be significantly predominant, it leads to a drop in the temperature of the eldest embryo which retards its development.

Our experiments involving sonification of embryos with clicks or tone signals simulating the vocalization of brood hens showed a notable reduction of the hatching time in all the studied species. We have observed different degrees of synchronization in different systematic groups, but the very existence of such synchronization is beyond any doubts (Table 2). Simultaneous hatching of the nandu, Galliformes and Anseriformes provides the opportunity for a quick removal of the hatch, consisting of numerous nestlings, from their nest as well as their prompt adaptation to the ecological conditions. It might be well to point out that the lengthiness of the hatching period observed in domestic species of Galliformes and Anseriformes in the process of commercial incubation is by no means a result of the fading ability to synchronization (Vince et al., 1970). This lengthiness can be explained as a lack of an important promoting factor: the vocalization of a brood hen and as a consequence of morphological heterogeneity of eggs in mass in the incubated parties which leads to morphological heterogeneity in embryos as well.

The results of our experiments have also shown that the acoustic stimulation promotes also the development of hearing sensibility inducing a certain lowering in the CM thresholds at the frequency of sonification (Fig. 4). The results of the histological investigations (the scanning electron microscopy) revealed that acoustic stimulation can produce selective acceleration in the maturation of the hair cells in the auditory epithelium which becomes evident, for example, in the growing number of stereociliums of these cells (Fig. 5).

Figure 6 presents a domestic duck in which one can see the interrelationship between the spectra of functionally significant acoustic signals and the development of hearing sensibility, its morphological basis being ensured by the growth of the cochlear auditory epithelium. It can be seen from the average CM characteristics that the development of hearing sensibility, involving the range from 0.2 to 2.5 kc. and having a functional importance for the behavioral reactions in the early ontogeny, is being accomplished in the course of the first stage, i.e. from the 14th to 24th days of the incubation. In this case these are the reactions of hatching synchronization, line of motion and approach to the source of the signal. On the top of the drawing there is a double line showing the functional importance of frequencies inducing the reaction of approach. The number of chicks responding to a definite frequency is expressed in per cent. As it can be seen, the effective frequen-

T a b l e 2. The influence of the acoustic stimulation of the synchronization of hatching in precocial and semiprecocial birds

| Systematic groups of birds | Quantity of eggs in the nest (or in the experiment) | The kind of stimulation | The time of hatching | |
|---------------------------------|---|--|----------------------|-------------|
| | | | Experiment | Control |
| <u>Anseriformes</u> | | | | |
| Anas platerinchos domesticus | 400 | Clicking | 17 h | 30 h |
| Somateria mollissima | 5 | Immitation of parent's call 400 Hz | 3 h 40 min | 9 h |
| Cygnus olor | 5 | Clicking | 6 h | 17 h 10 min |
| <u>Gaviiformes</u> | | | | |
| Gavia stellata | 2 | Clicking | 22 h | 39 h 30 min |
| Gavia arctica | 2 | Clicking | 18 h | 41 h |
| <u>Podicipitiformes</u> | | | | |
| Podiceps cristatus | 4 | Clicking | 26 h | 47 h 40 min |
| Podiceps griseigena | 4 | Clicking | 28 h 20 min | 52 h 30 min |
| <u>Rallidae</u> | | | | |
| Fulica atra | 9 | Clicking | 36 h | 58 h 50 min |
| Gallinula chloropus | 7 | Clicking | 32 h 20 min | 54 h 30 min |
| <u>Charadrii</u> | | | | |
| Tringa totanus | 4 | Immitation of parent's call 800 Hz | 21 h | 37 h 15 min |
| Charadrius dubius | 4 | " 1400 Hz | 18 h | 32 h |
| <u>Laridae</u> | | | | |
| Larus canus | 3 | " 800 Hz | 49 h 40 min | 75 h 25 min |
| Sterna paradisaea | 2 | " 1400 Hz | 32 h 20 min | 54 h |
| <u>Alcidae</u> | | | | |
| Cepphus grylle | 3 | Clicking | 34 h | 56 h 30 min |

cies are presented in the range from 0.3 to 2 kHz. The correlation in the development of hearing sensibility associated with the manifestation of behavioral reactions becomes evident. Similar results have been obtained when studying the reactions of hatching synchronization along with the feeding reaction in nudiformes. It is believed that the acoustic channel of the starting stimuli in the most important functional systems of the early ontogeny is formed just in the course of the first stage. We can point out that the lowering of CM thresholds from the 20th to the 24th days after the incubation occurs at the frequencies corresponding to the spectrum of the first pippings of embryos to be detected since the 25th day after the incubation. The progress in the hearing sensibility at a higher range creates certain prerequisites for the development and stabilization of more complicated forms of acoustic communication including recognition and differentiation of the parents' signals. Com-

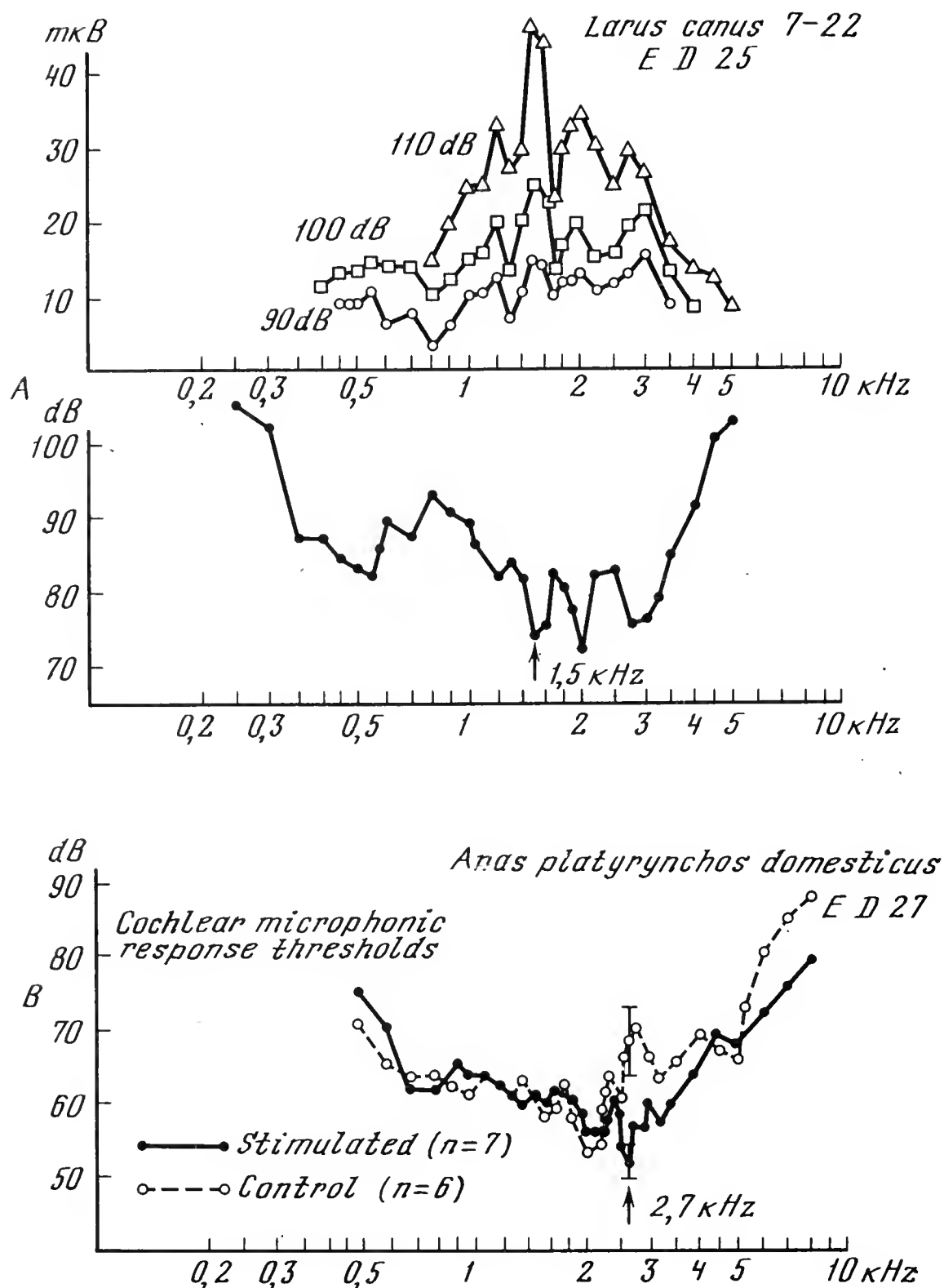
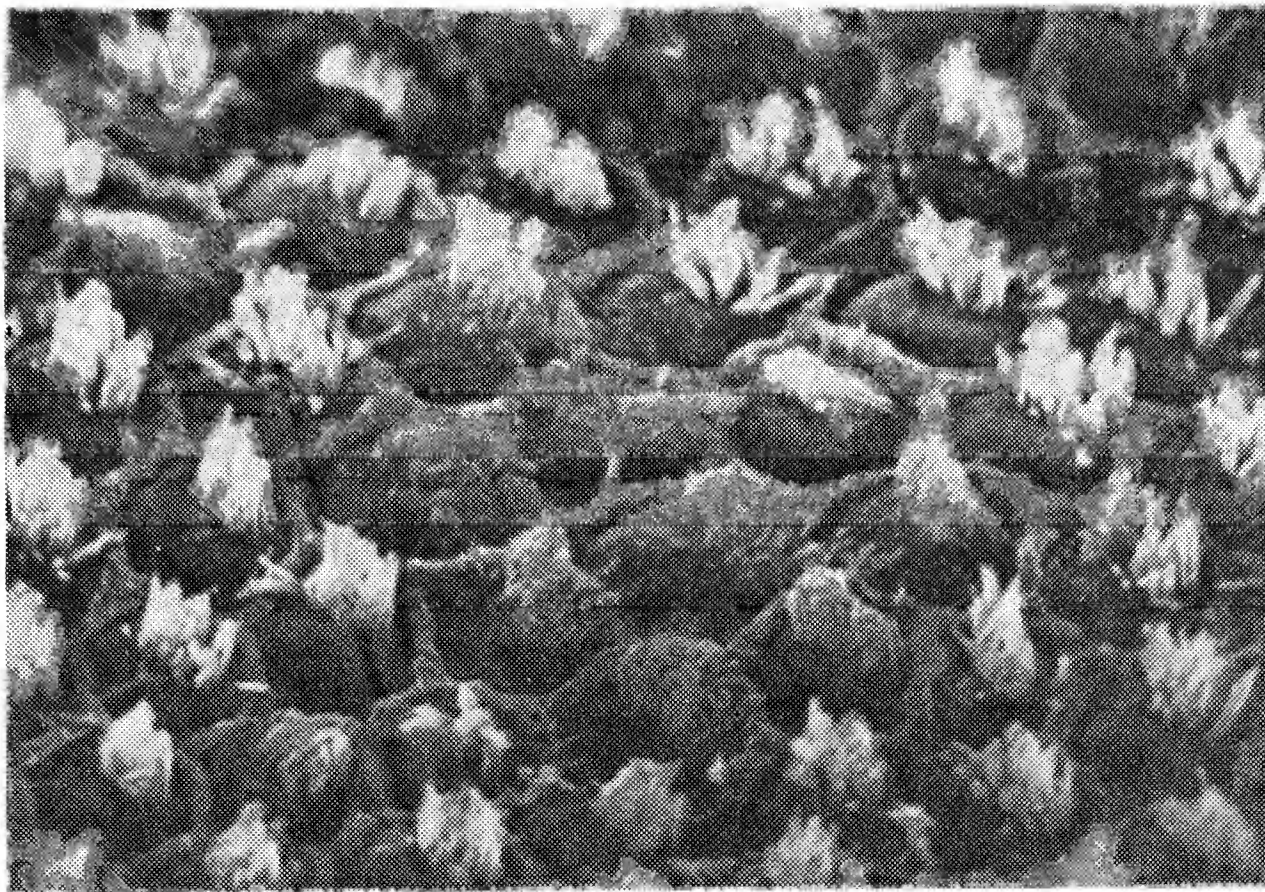


Fig. 4. The influence of the acoustic stimulation on embryos' CM characteristics

A - the frequency-amplitude CM characteristics (mkV) and CM thresholds (dB) of *Larus canus* embryo D 23, which was stimulated by tone 1,5 kHz (at 90 dB SPL, the duration of impulses 200 ms, 4 per sec, for 30 min every 2 hours, during 30 hours)

B - CM average thresholds of sonificated and control *Anas platyrhynchos domesticus* embryos before hatching. The experimental embryos were stimulated by tone 2,7 kHz (at 80 dB SPL, the duration of impulses 200 ms, 15 min every 2 hours, 20 times). Vertical bars - confidence interval at 10% significance level

paring the spectrum of signal of the brood hen with the CM threshold characteristics of embryos before their hatching. it is easy to note a correlation of their ranges. A very distinct correlation can be observed between the region of maximal sensitivity of the CM threshold characteristics of embryos before the hatching and the spectra of their own signals.



F i g. 5. Scanning electron microphotograph of hair cells surface in the middle-apical region of papillae basilaris of Anas platyrhynchos domesticus embryo D 21 illustrating the influence of acoustic stimulation. View from the side of cartilage. The embryo was stimulated by tone 1,3 kHz (at 90 dB SPL, the duration of impulses 200 ms, 2 per sec, 20 min every 2 hours, during days 19-21 of incubation). Acoustic stimulation produced increasing of cell surface size and growing number of stereocilia in several groups of cells, one of which is presented on the picture (seven cells in the middle of the picture have 72-92 stereocilia while the neighbouring cells have 42-52 stereocilia). x 4000

Our data on the maturation of the cochlear auditory epithelium correspond to the processes of development of the hearing sensibility and assimilation of the frequency range. The maximum rate of growth of epithelium in the duck is registered from the 25th to 27th days since the incubation, i.e. during the second stage (Fig. 6C).

The state of the auditory receptor epithelium in the embryos of domestic duck since the onset of functioning of the acoustic analyzer (the 15th day after the incubation) and the one before the hatching are depicted in Fig. 7, 8.

Until the present time there is an unsettled discrepancy in the notion on the interrelation between the structure and the function of the evolving cochlea. It may be presented in the following way. It is known from the data of histological investigations that maturation of the auditory epithelium begins from the basal end. Proceeding from the present-day concepts of hearing physiology it is clear that the claim on the primary maturation of the basal end of the auditory epithelium is equivalent to the statement on the primary perception of high frequencies. However, it is evident that in birds as well as in mammals the sensibility to perceive low frequencies is manifested since the onset of functioning of the acoustic analyzer. It should be stressed that the birds' cochlea tonotopy is left as an unsolved problem, and it may be

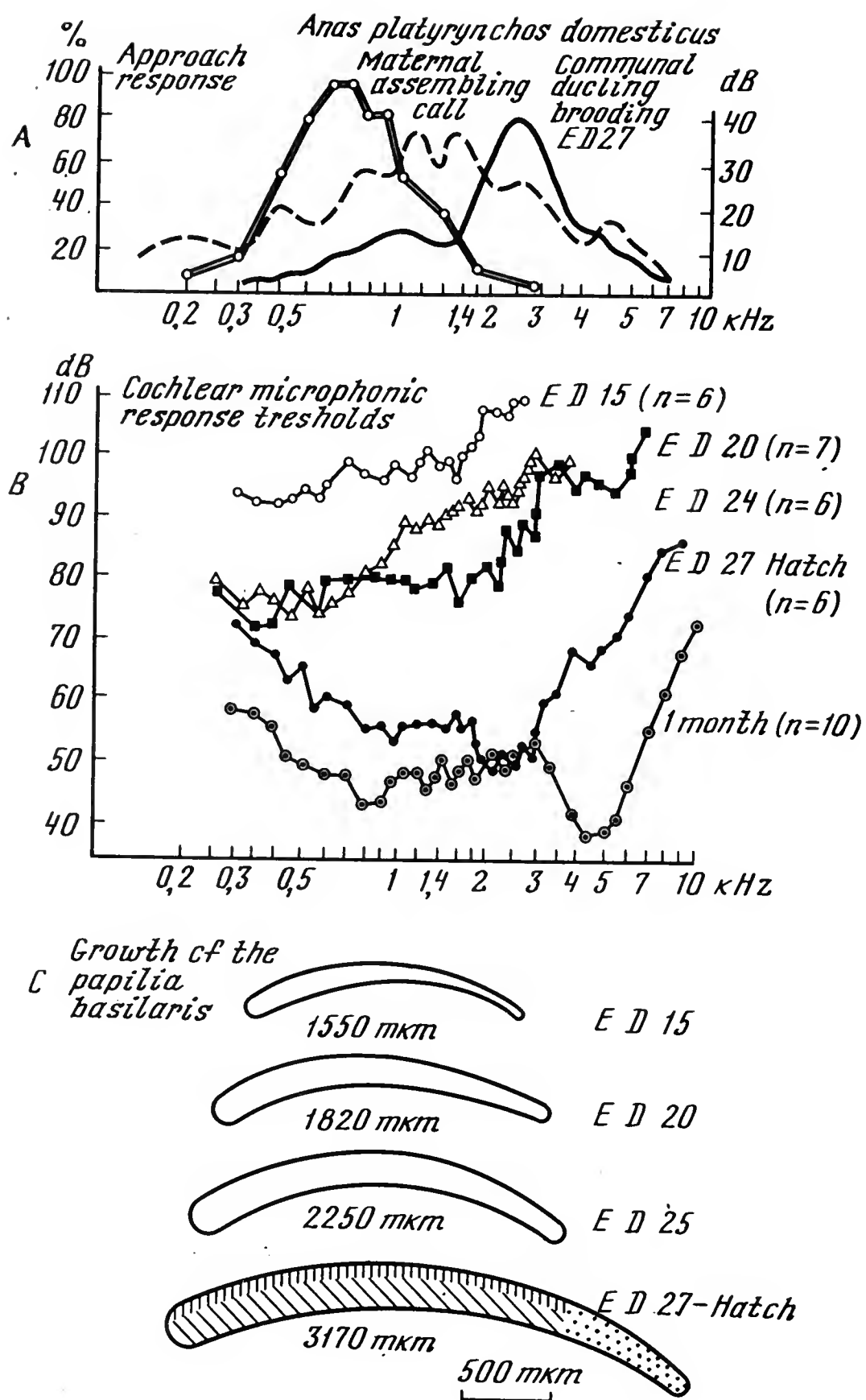
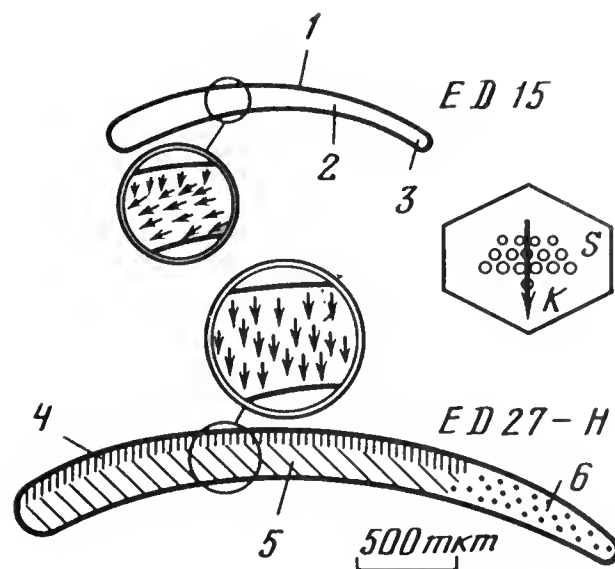


Fig. 6. Correlation between the functional meaning of tone signals in the approach response of ducklings (A, %, double line), spectra of duck's maternal and ducklings acoustical signals (A - dB, from G. Gottlieb, 1971) and the development of CM thresholds in duck embryos and ducklings (B). C - growth of the papillae basilaris during embryogenesis. Vertical lines area illustrates region of tall hair cells on the cartilage, the slanting lines area - region of jug-shaped cells on free basal membrane and the dotted area - cup-shaped cells in the basal region. The figures under papillae are represent the length of the pappilae basilaris. The fastest growth of pappilae basilaris takes place during the second stage of hearing development: D 25-27 of incubation

Fig. 7. Schematic drawings illustrated kinocilial orientation patterns in duck embryos papillae basilaris and the locations of examples (1-6) are given Fig. 8



only tentatively admitted that the midapical sector of the auditory epithelium is apparently liable for the perception of low and medium frequencies, and the basal sector - for high frequencies.

We discriminate three types of hair cells in the cochlear auditory epithelium of adult birds: the tall and jug-shaped cells are situated in the midapical sector of the auditory epithelium, the tall cells - on the cartilage, the jug-shaped ("short") ones - on the free basilar membrane (Takasaka, Smith, 1971; Yamalova, 1977), and the cup-shaped (lenticular) cells occupying the basal sector of epithelium (Yamalova, 1977; Prokof'eva, Yamalova, 1978, 1979; Takanaka, Smith, 1978; Golubeva, Yamalova, 1980). It so happened that the cup-shaped cells of the basal sector escaped the notice of investigators for a long time, and they have been described only recently. Their number amounts to no more than 5-6% of the total number of the auditory hair cells though the basal sector occupies nearly one third the length of the auditory epithelium: the basal sector is relatively narrow and the apical surface of the cup-shaped hair cells is extensive. For example, in the adult duck the basal sector contains about 400 cup-shaped hair cells, the total number of the auditory hair cells amounting to 8000.

Our investigations have shown that since the onset of functioning of the acoustic analyzer (in the duck it is the 14-15th day of embryogeny) the hair cells exhibit the greatest development over the area of 95 to 50% the length of the receptor epithelium (counting from the apical end). As this takes place one can reveal both the basal-apical gradient of the degree of maturity of hair cells and the apical-basal gradient in the very basal end taking up approximately 5% the length of the whole epithelium. The differentiation of the hair cells in the apical direction proceeds very fast. Besides these longitudinal gradients of differentiation and maturation of the hair cells there is also a transversal heterochronia. The cells exhibiting the fastest rate of maturation (jug-shaped) are situated in the region of transition of the auditory epithelium from the cartilage to the free basilar membrane. We have discovered a basic feature of these differentiating hair cells which mature prior to all the others. It is well known that in adult birds the orientation of all hair cells is identical: their kinocilia are directed towards the outer border of epithelium (towards the outer cartilage). Since the very onset of functioning of the acoustic analyzer all the hair cells, excluding the cells of



F i g. 8. Scanning electron micrograph of the tall (1,4), jug-shaped (2,5) and cup-shaped (3,6) cells in domestic duck embryos

1, 2, 3 - in the beginning of the first stage of hearing sensitivity development (embryo D 15), 4, 5, 6 - in the end of the second stage (embryo D 27). x 6000

the basal end-point and from 2 to 6 rows of cells along the border of epithelium on the cartilage, are oriented so that their kinocilia are directed towards the apical end of epithelium (Fig. 7). Since the very onset of their differentiation the hair cells in the basal sector and the extreme tall hair cells on the cartilage have the orientation which is typical of adult cells. The stereocilia of hair cells oriented towards the apical end from comparatively even rows disposed at the right angles to the auditory epithelium. Soon these rows undergo changes assuming the S-shaped form of their lines. The change in the orientation of these hair cells is apparently stipulated by two processes: 1) different rates of growth of the apical surface of the central and outer hair cells and 2) dislocation of the ciliary apparatus in each cell. At the end of the first stage in the development of hearing (in the duck it is by the 24th day of embryogeny) the turn of the hair cells is completed. We have detected a change in the orientation of the hair cells in all the studied species, and this enables us to presume a change in the trend of the effect of the excitative stimulus in the cochlea at an early stage of the development of hearing. It seems obvious that this conclusion corresponds to the hypothesis on a change in the frequency tuning of the hair cells differentiating prior to all others in the course of ontogeny (Rubel, 1978).

Despite the fact that the cup-shaped hair cells of the basal sector are differentiated prior to the hair cells of the cochlea apical end, the process of their maturation takes the longest time. By the end of the first stage of the development of hearing their number in the basal sector amounts to the number common for the adult cells, and at this time the basal sector accounts for 20% of the total auditory epithelium owing to the prompt growth of their apical surface. In the Peking duck the cup-shaped hair cells become fully mature only by the end of the third stage. At the time of hatching they are still relatively immature (as also are the extreme tall hair cells) which is proved by the presence of microvilli on their surface (Fig. 7). In our opinion this offers an opportunity to correlate the maturation of the cup-shaped cells in the basal sector with the formation of sensibility to the high frequencies (Fig. 6).

It should be emphasized that with the leading development of the jug-shaped and hair cells one can observe also more special cases of intratypiform heterochrony in all auditory hair cells. This phenomenon is expressed to a variable degree in different species, and it is especially clearly pronounced in gulls (Golubeva, 1980). We believe that the manifestation of this heterochrony in the maturation of hair cells is revealed in the CM characteristics of the gulls' embryos provided with several narrow regions of maximal sensitivity and separated by the regions with high thresholds.

It follows that the three stages of the development of hearing sensibility in birds are interrelated with certain morphological characteristics of the developing auditory epithelium. The existence of the three stages represents a general regularity inherent in all species of birds. However, the specific features characterizing the development of hearing of every given species are determined first of all by ecology. In this process the most important role is played by the species-specific vocalization which, on the one hand, is rigorously governed itself by the ecological conditions and, on the other hand, exerts direct effect upon the formation of hearing sensibility.

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ACOUSTICAL RECEPTION IN BIRDS

A.N. Temchin

Department of Vertebrate Zoology, Moscow State University, Moscow, USSR

Modern concepts on the mechanisms of acoustic reception have developed on the basis of studying the functions of inner ear in mammals and man. Scarce studies carried out on representatives of other classes of vertebrates do not contribute any essential details. Meanwhile, the peculiarities of morpho-functional organization of avian acoustic receptors require a cautious approach when applying generally accepted concepts of peripheral analysis to this group of vertebrates. A systematic microelectrode study of the properties of auditory nerve fibres in birds (pigeon) has revealed some previously unknown phenomena which appear to be of principal interest for the problem of acoustic reception in vertebrates.

These studies were carried out on the pigeon Columbia livia, a species with generalized hearing. The method of denudation of the auditory nerve developed made it possible to record the impulse activity of single fibres with glass micropipettes. All other details of the method did not differ from those of the routinely used one. The spike activity of the auditory nerve fibres (ANF) was treated directly in the course of experiments with a multi-channel analyzer NOKIA LP4840. The results given below are based on studies of 1000 ANF of pigeon.

One of the first results concerned the spontaneous ANF activity or, to be more precise, the temporal distribution of this activity in different fibres. It is well known that the spontaneous activity of single fibres of the auditory nerve in mammals is random and its interspike distribution agrees with the Poisson's law (Sachs et al., 1974; Walsh et al., 1972). Meanwhile, two thirds of the pigeon ANF have shown interspike distributions which differed markedly from the random one and were characterized by the appearance of "additional" modes on the histogrammes of interspike intervals (Fig. 1). Any such "additional" mode indicates to the existence in real sequence of spontaneous pulses of a certain excessive (with respect to the random one) number of intervals of different length. "Periodical" histogrammes of spontaneous activity, with their modes separated by the same time intervals, registered in a great number of ANF were the most spectacular demonstration of this phenomenon (Temchin, 1980).

These results suggested the existence of rhythmic oscillations of excitability on the fibre within the real time scale which were then studied by means of autocorrelation functions. They proved to be different in the ANF with different spontaneous activity (Fig. 2). If the distribution of interspike intervals was strictly Poissonian (Fig. 2, A), the probability of the spike spontaneous generation did not change in time, thus corresponding to a random process (Fig. 2a), whereas in the periodical histogrammes (Fig. 2, B, C, D) this probability increased regularly when the time was multiple to the period of interpulse histogramme (Fig. 2, b, c, d). This latter result allowed one to suggest that the polymodality of temporal distribution of spontaneous activity on any fibre is due to rhythmic oscillations of the membrane potential of the corresponding hair cell. In this case, the appearance of a spike

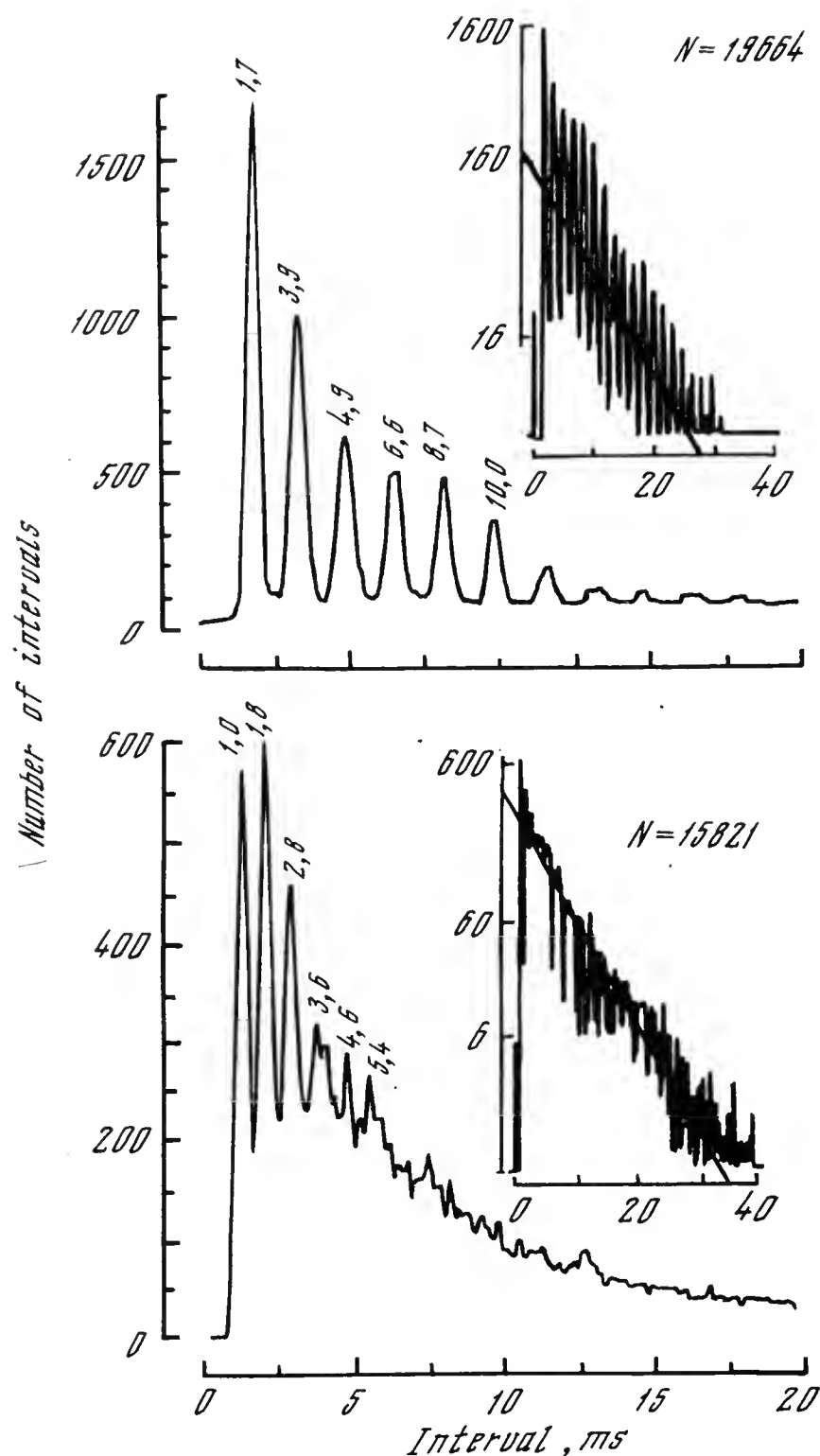


Fig. 1. "Periodical" interspike interval histograms for the spontaneous firing in two auditory nerve fibers. Each histogram is based on discharges which occurred during 100 s and present in linear and semilogarithmic scales. Bin = 100μ s. "N" is total number of intervals in each histogram. The former of six modes of each histogram indicated in ms

in its innervating fibre proves to be the most probable in those moments which correspond to the maximal depolarization of the hair cell. Under such conditions, any interspike interval in the fibre will be predominantly multiple to the period of the membrane potential oscillations, which is reflected on the corresponding histogrammes in the form of "periodical" distribution of their modes.

In different ANF the values of these periods varied from 0.45 to 8.5 msec, but they proved to coincide closely with those of their characteristic frequencies. Thus, an important property of "periodical" fibres was discovered: their characteristic frequency corresponded to the period of oscillations of the membrane potential of the hair cells which they innervate. Taking into account the minimal registered value of the period of interpulse histogrammes (0.45 msec), it becomes clear that the phenomenon described is inherent to low frequency fibres, whose characteristic frequencies do not exceed 2.2 kHz.

It should be noted that the phenomenon of periodicity of spontaneous impulsation in the avian ANF was independently and simultaneously described by Manley (1978), and our hypothesis concerning spontaneous oscillations of the membrane potential of the hair cell (Temchin, 1980, 1982) taking place with characteristic of the given cell frequency was directly confirmed by Craw-

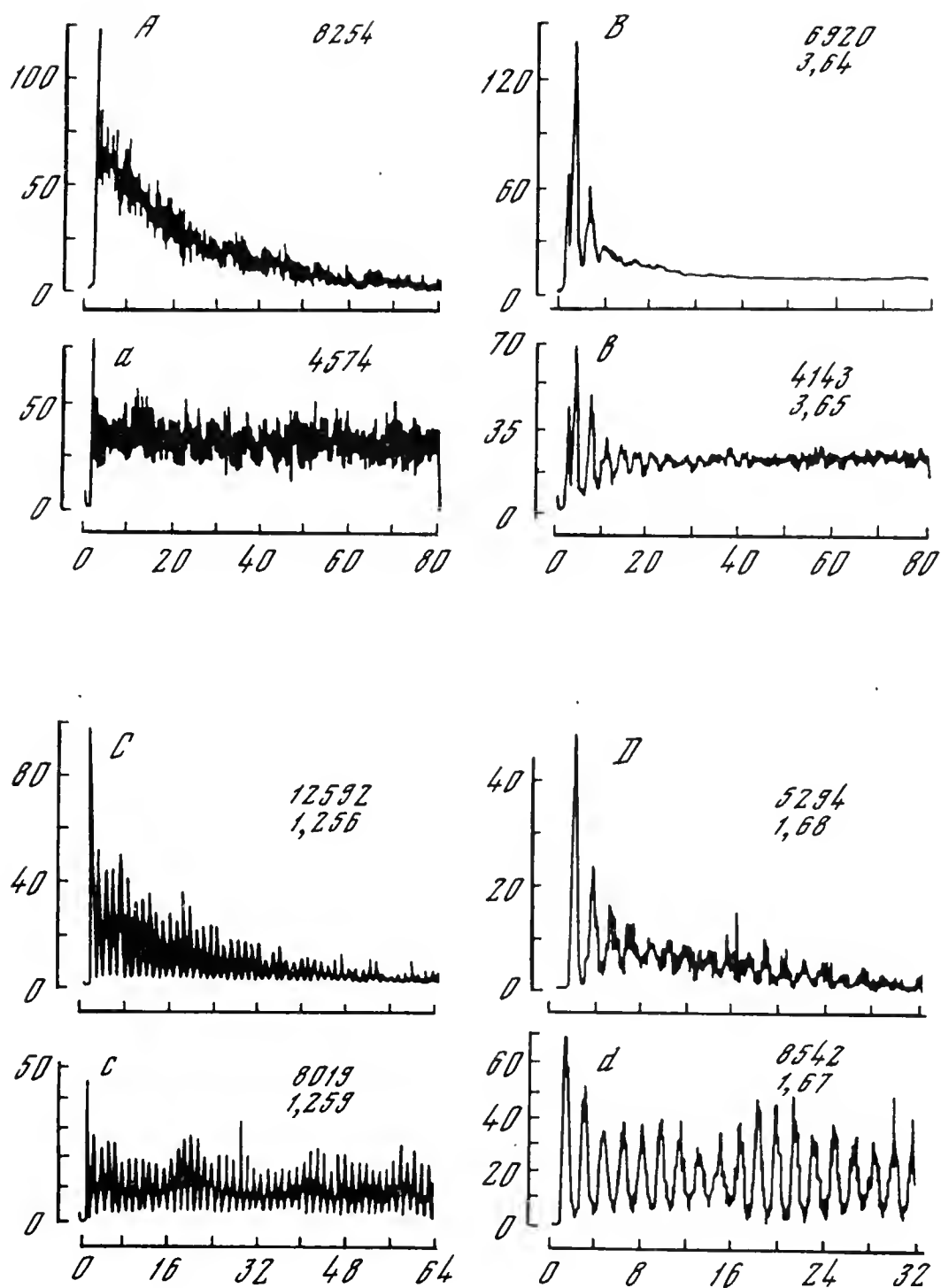


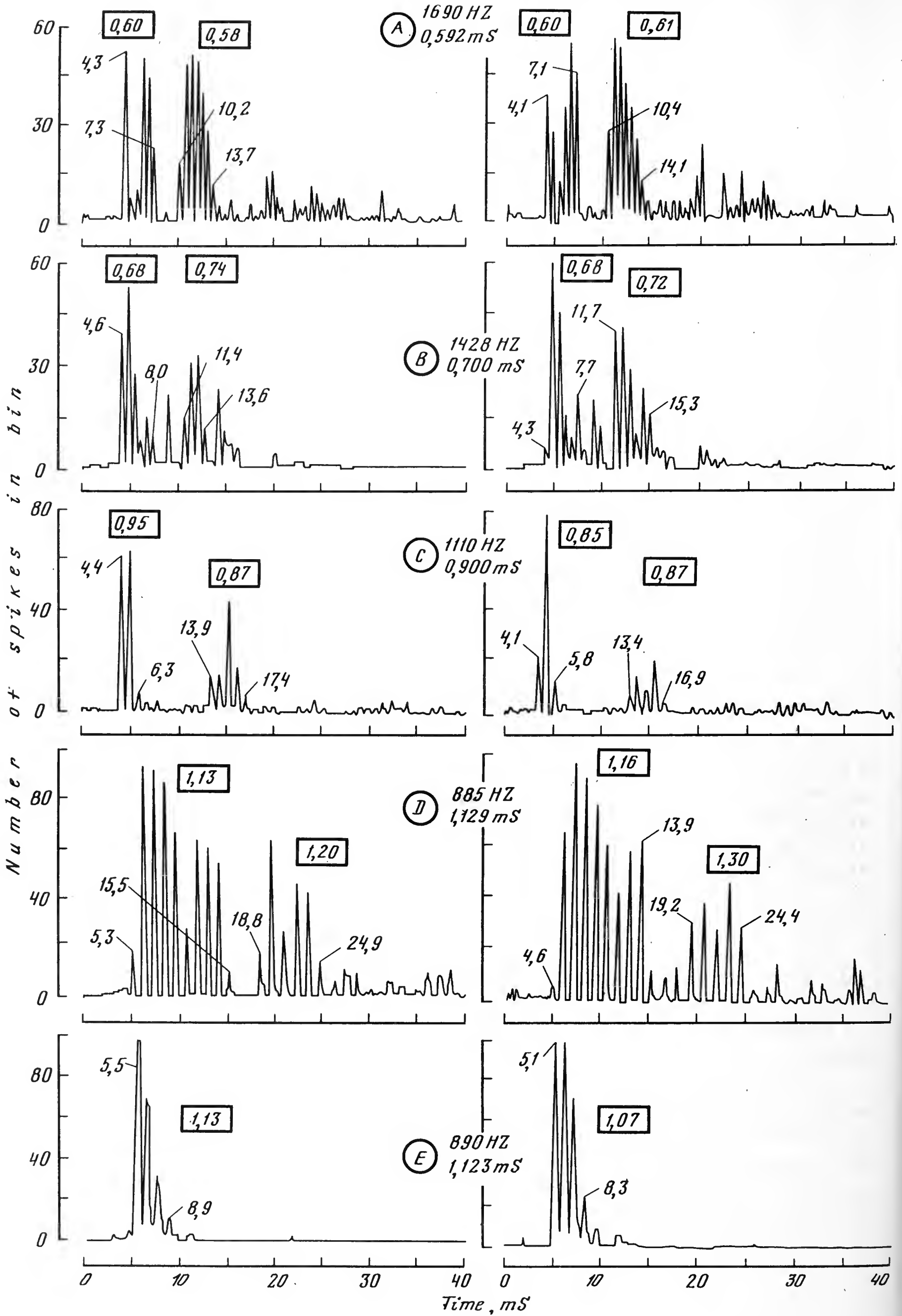
Fig. 2. Interspike interval histograms for the spontaneous firing in four auditory nerve fibers (A-D) and their autocorrelated functions (a-d) accordingly. The condition of experiments and coordinates as on Fig. 1. Bin=100 μ s (A, a, B, b) and 40 μ s (C, c, D, d). The numbers in corner of each histogram from the top: total number of intervals (A-D) or number of step correlation (a-d) and period of each histogram in ms

ford and Fettiplace (1980). They found that the membrane potential of hair cells in the turtle varied within the limits of a few msec and the frequency of these variations coincided with that of the maximal response of these cells.

The majority of low frequency fibres of the auditory nerve in the pigeon are, thus, characterized by spontaneous impulsation whose temporal structure reflects the characteristic frequency of the given fibre. Since these results were obtained under conditions of complete silence (in a large sound-proof chamber) and oscillations of the membrane potential proceeded spontaneously, there are good grounds to consider this phenomenon as an expression of "electrical" tuning of the hair cells. This allows one to regard the hair cell as

Condensation

Rarefaction



an actively tuned cell rather than a passive mechanoreceptor, as was considered previously, its electrical properties corresponding to the mechanical ones of the basilar membrane locus on which the given hair cell is located.

As to ANF reactions to different acoustic stimuli, their PST histograms upon presentation of a shortterm click are worth noting. As is well known, the same reactions of mammals are always of monotonously attenuating character. But these very reactions of the pigeon ANF were characterized by a greater duration, diversity of temporal organization and appearance of a pack pattern in their responses in a great number of fibres (Fig. 3). The diversity of responses could be observed even in the ANF whose characteristic frequencies were rather close, thus suggesting that the mechanical phenomena occurring on the functional properties of individual fibres. It is suggested that the demonstrated diversity of these reactions is related to the specific features of local electrical processes which develop on a particular hair cell and are due to the morphological contacts of the cell itself and its innervations (Golubeva, 1980). This hypothesis is confirmed by the pack pattern of response, while it is evident that the mechanical processes of the corresponding cell of receptor epithelium, upon pulse stimulation, have to attenuate due to constant, in terms of time, expenditure of stimulus energy. Different types of temporal organization of the response of the same fibre to the stimuli of compression and rarefaction serve as another confirmation of receptor epithelium participation in processing information. As is known from literature on the subject, in this case it is only the sequence of phases of de- and hyperpolarization of the hair cell which changes. However, the above differences in the fibre pulse reactions are due not so much to their temporal shift as to the reorganization of the reaction itself. ANF with low characteristic frequencies proved to be the most diverse.

The character of the reaction itself to the click was determined by the fact that the receptor epithelium locus, with which the given fibre is connected, begins to oscillate with a frequency of its own and the cell potential suffers a change of de- and hyperpolarization phases with the same frequency. In agreement with these processes the origin of spike is timed to the moment of hair cell depolarization, and the PST histograms become periodical as a result. This concept is confirmed by the coincidence of the period of PST histograms with that of the characteristic frequency of the fibre under study.

Furthermore, some data on spatial localization of frequencies in cochlea can be obtained by comparing the latency of these reactions and the characteristic frequencies of the corresponding fibres since it is known that the value of the latent period of mechanical propagation along the basilar membrane. Such a distribution proved to be characterized by a dispersion of la-

Fig. 3. Responses of five auditory nerve fibers (A-E) to condensation (left) and rarefaction (fright) clicks (500 presentation in each case). Bin = $100 \mu s$. The numbers between histograms are F_0 in HZ and period F_0 in ms. The numbers in frame above histograms are periods of the response firings in ms. Some modes of histograms indicate in ms

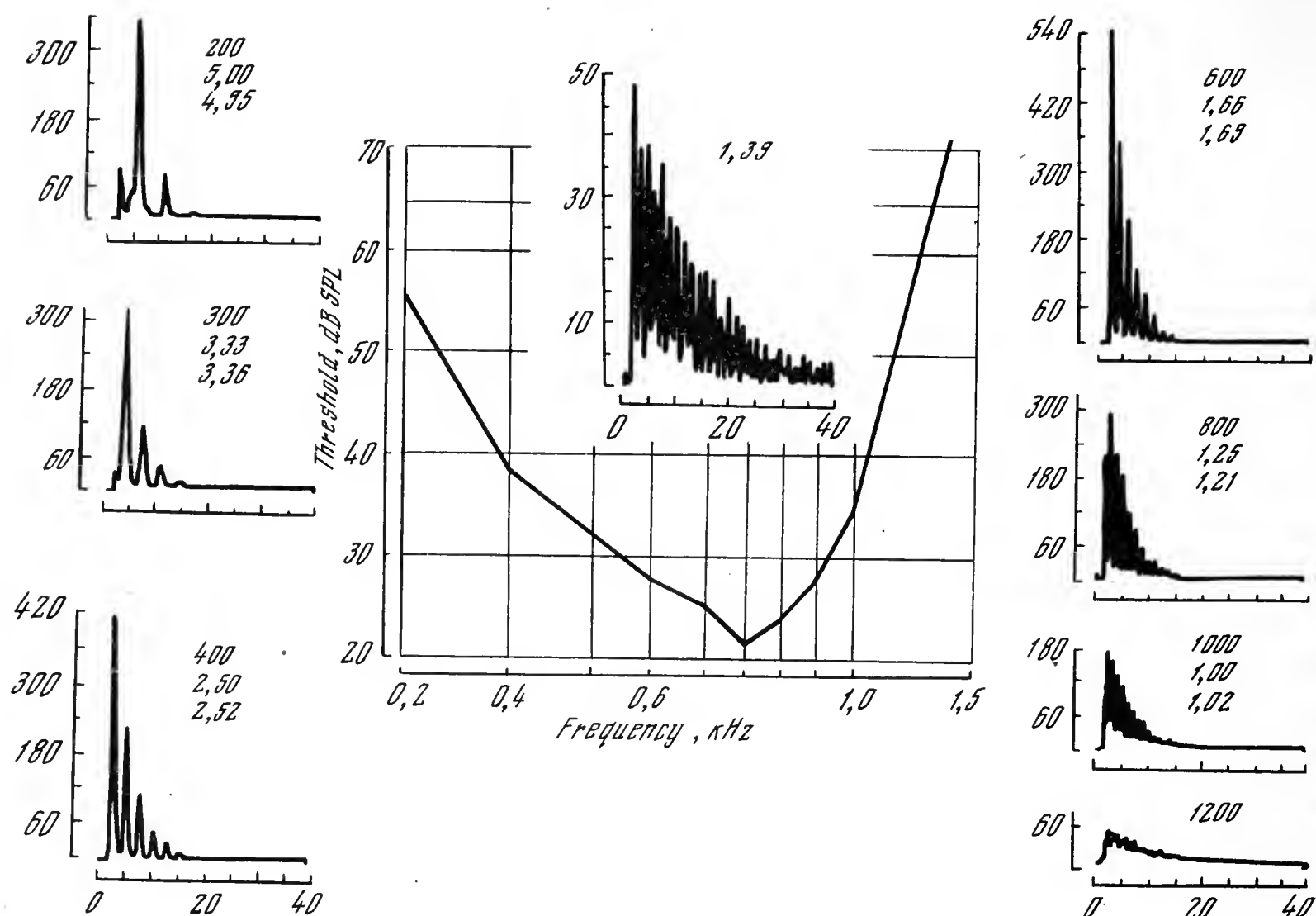


Fig. 4. Frequency-threshold curve of the auditory nerve fiber (in center) and interval interspike histograms of the responses this fiber to 5 tone burst (duration 10 s). The numbers in corner of each histogram from the top: frequency of stimuli in HZ, its period in ms and period of histogram in ms. Above FTC there is interspike interval histogram of spontaneous firing this unit (50 s) and its period in ms

tent periods, expressed especially in the low frequency portion of the spectrum. One can believe that this result reflects a more complicated localization of frequencies in the avian cochlea than on the mammalian basilar membrane.

The stimulation of the pigeon ANF with tonal stimuli of optimal frequencies induced uniform enough reactions whose duration coincided with that of the stimulus, and the temporal structure was ordered in accordance with its frequency (Fig. 4). This type of response, as in the former case, was determined by a constant change of the sign of cell polarization arising upon oscillatory movement of receptor structures. The appearance of action potentials was shown to be the most probable upon the rarefaction wave on the tympanic membrane which induced hair cell depolarization while the compression wave hyperpolarized the cells, thus inhibiting the fibre, as was distinctly seen on the poststimulation histogrammes in a semilogarithmic scale.

These regularities account for the phase coincidence of discharges found in the whole range of optimal, for the given fibre, frequencies. It is clear that the interspike intervals at different frequencies reflect unequivocally the value of the period of stimulating frequency in the whole range of the work of this fibre. This peculiarity is expressed at any intensity of the stimulus, including nearthreshold ones.

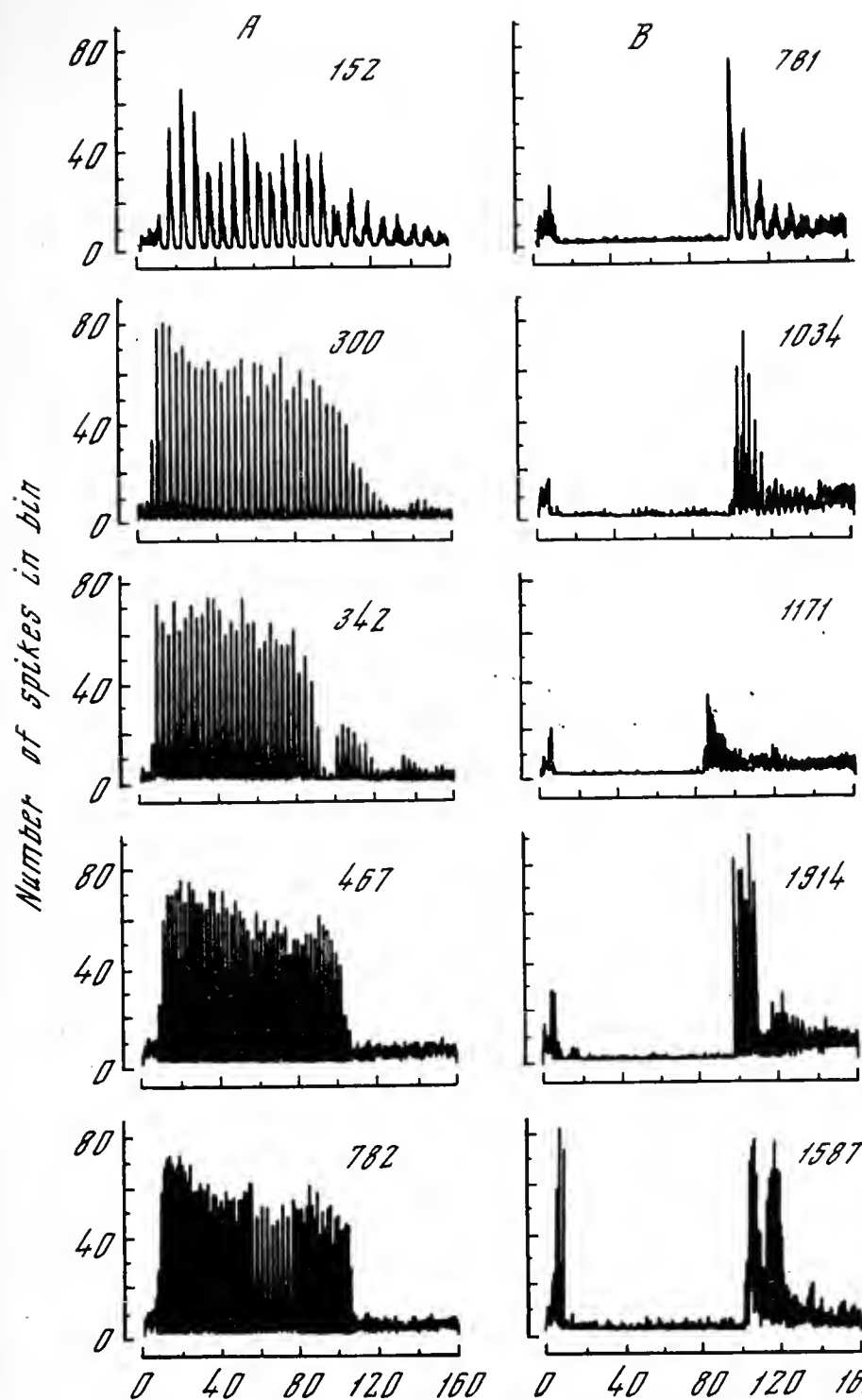


Fig. 5. Excitation (left) and inhibition (right) responses of five auditory fibers. 500 presentations 100 ms tone burst frequencies of which are indicated in the corner of each histogram in Hz. Bin = $100 \mu s$

The characteristic frequencies of the pigeon ANF lay within the range of 0.1 to 5.0 kHz although the highest frequency particles were rather difficult to find. They were of usual form and their quality factor (Q) varied from 0.8 to 8, i.e. markedly exceeding the mechanical quality of the basilar membrane known from literature. The idea of a "second filter" seems the most promising for the explanation of this intensification.

The tonic type of response described, the only known for mammals proved to be not the only one. Another type of reaction, previously unknown in literature, was found in a considerable number of fibres upon stimulation with frequencies, markedly exceeding the optimal ones (Fig. 5). Their form was similar enough in different fibres and was characterized by a suppressed on-reaction with a short latency, a fall of impulsation frequency during the stimulus action, and a powerful off-reaction in its end, which had the character of attenuating oscillations. The application of long-term stimuli resulting in the suppression of fibre spontaneous activity was shown to be unaccompanied by its adaptation and the intracranial dissection of the auditory nerve did not change these reactions. We registered, thus, the monofrequency afferent inhibition of the auditory nerve fibres in the pigeon, a phenomenon previously unknown for this level of acoustic system in vertebrates.

The necessary condition of the expression of fibre inhibitory properties

consisted in the presence of periodicity in its spontaneous activity, and vice versa: the zone of inhibition was always found in all ANF with such periodicity.

SUMMARY

A study of 1000 pigeon auditory nerve fibers, with the use of microelectrodes, revealed periodicity of their spontaneous activity, determined by a fiber's best frequency. This phenomenon is determined by electrical tuning of a hair cell and is related to spontaneous oscillations of its membrane potential. Click responses showed a diversity that cannot be explained in terms of narrow - band filtration, but presupposes electrical interaction between neighbouring hair cells. A considerable latency dispersion suggests that spacefrequency relations in avian cochlea are different from those in the mammalian ones. Response to tonal stimuli showed a phase - locking up to 4 kHz; their character can be explained by a successive change of a de- and hyper-polarization of a hair cell. Stimulation by higher frequencies led to afferent inhibition that was due to a long hyper-polarization of a hair cell. A study of time-pattern of inhibitory responses showed that they were related to mechanical disturbances different from those determining excitation responses of the same fiber.

The data presented are discussed from the point of view of both peripheral coding in Aves and general mechanisms of reception in the lateral-acoustic system of vertebrates, related to electrical tuning of receptor structures.

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THEORETICAL ASPECTS OF AVIAN NAVIGATION

Hans G. Wallraff

Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, FRG

Theoretical considerations, if they shall stay in contact with the real world, cannot be isolated from empirical research. Thus, dealing with theoretical aspects of avian navigation can only mean emphasizing these aspects, yet experimental confirmation or disproof of theoretically possible mechanisms has to be mentioned in addition. Within the limited space, only rough outlines can be given, and the more interested reader has to be referred to the quoted literature.

ORIENTATIONAL MECHANISMS IN MIGRATION

The periodic movements between breeding and wintering areas, occurring year after year in many species, most extensively and impressively demonstrate the navigational capabilities of free-living birds. In order to analyse these capabilities, we should consider which variables potentially might determine the specific kinds of movements. In a most simple approach, we can divide the migratory system of a population into three parts (Fig. 1A): the breeding area, B, the wintering area, W, and the area covered by the migratory routes, R, connecting B and W.

For a young bird hatched at B, it may be sufficient to be informed, by phylogenetic transmission, on either R or W, yet not necessarily on both. Depending on R appears to be the simpler way, as the bird only needs to know an intended angle in relation to some environmental direction of reference. Any feature providing sufficiently steady azimuth information within the whole living area of the population is suited as a reference for the resulting compass orientation. From the few features of that sort existing, astronomical cues (stars, sun) as well as the magnetic field of the earth are known to be utilized by birds (e.g., Emlen, 1975; Schmidt-Koenig, 1979; Able, 1980). Different compass systems have different advantages and disadvantages, and this may affect the interrelations between them (cf. Wallraff, 1977, 1978b). In this volume, Wiltschko and Wiltschko report on empirical research that has been done to clarify these interrelations as well as the way in which population-specific intended directions of migration are genetically encoded (see also Bingman, 1981; Wiltschko, 1982; Beck, Wiltschko, 1982). The field appears rather complex and definite answers require further investigation.

By following its spontaneously intended compass direction, the young bird automatically reaches the wintering area W (Fig. 1B). However, we still have to ask for the determinants causing our bird to end its journey just in the area W and not somewhere before or behind. Such determinants could either be local or temporal in nature, or they could result from some measurement of the distances covered (for more details see Wallraff, 1972, 1977). Convincing experimental evidence so far exists for an endogenous temporal program which determines the where-to-stop by means of a population-specific where-to-stop (e.g., Gwinner, 1968, 1977; Berthold, 1973).

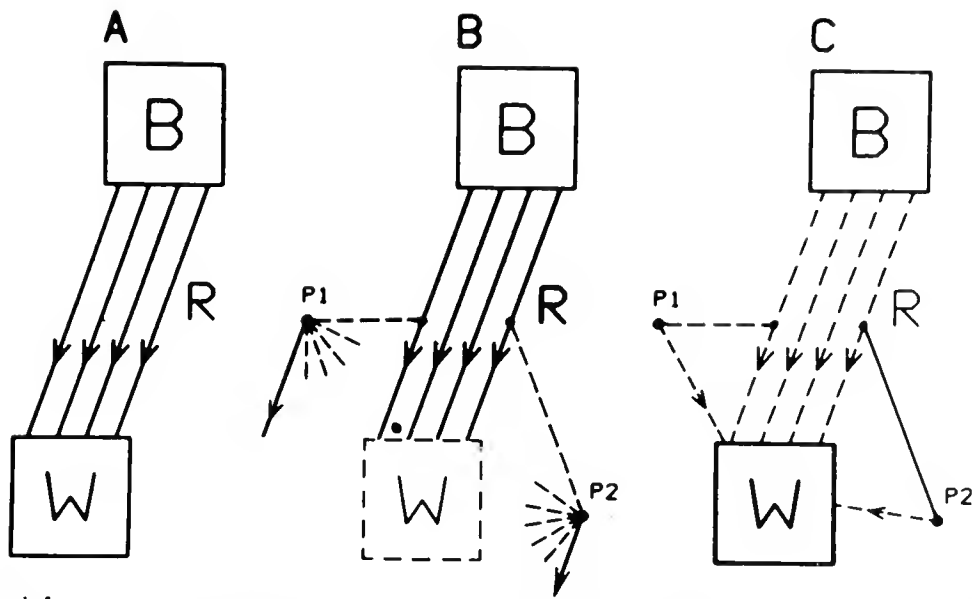


Fig. 1. Schematic presentation of breeding area B, migratory routes R, and wintering area W. A - descriptive scheme of autumn migration; B - birds are informed of compass direction of R, but not of goal area W. Displacements to sites P1 and P2 result in flights parallel to R; some course correction towards the original R domain or its elongation may occur. C - birds are informed of geographic position of wintering area W. Displacements to sites P1 and P2 result in goal-oriented flights towards this area

Together with some selectiveness for ecologically appropriate habitats, a direction-and-distance (vector) system involving some flexibility may be sufficient to explain most of the simpler broad-front migratory pathways. Even in those cases, however, the system may include mechanisms against interfering disturbances like wind drift or landscape barriers acting as deflection lines (a term that often appears more appropriate than the classical "leading line"). Such correction mechanisms may include elements of goal orientation (see below), but need not include localization of the wintering grounds (cf. Wallraff, 1972; Wiltschko, 1973). Necessarily more complicated is the equipment of those birds whose migratory routes are more specifically adapted to the geomorphological structures of the continents. The list of mechanisms that theoretically may render such routes possible (Wallraff, 1977) is not yet noteworthy shortened by empirical research. The most convincing indications concern, again, a temporal program in which changes of the migratory direction are comprised (Gwinner, Wiltschko, 1978).

The alternative to a migratory system based on direction and distance is position-finding by true goal-oriented navigation. In this case, the bird would not follow an intended compass direction; rather it would be informed in some way on the geographic position of its goal which it then should be able to reach from everywhere (Fig. 1C). Such systems are known to exist, yet all indications thus far available support the conclusion that a site or area acting as a goal must previously have been experienced by individual presence (e.g., Perdeck, 1958). Thus, goal-oriented navigation always appears to be some sort of homing (yet different speculations are sometimes expressed; see Rabøl, 1969, 1978).

Under natural migration conditions pure position-finding as shown in Fig. 1C may scarcely occur, as even the adult birds, which may have imprinted B as well as W as "home areas", still should be aware of their population-

specific intended compass direction. The result should be a combination of the types shown in Fig.1, B and C. Particularly in long-distance migrants it may well happen that even the adults still depend on pure compass orientation for performing their transcontinental or intercontinental flights and that goal orientation comes into action only at the later stages of the journey.

MECHANISMS OF GOAL-ORIENTED NAVIGATION

Position finding can be investigated at best by homing experiments which commonly involve passive displacement to more or less distant sites. Such experiments have most extensively been conducted with homing pigeons, so that our more detailed knowledge mainly concerns this domestic bird. So far, however, there is no reason to suppose that wild species navigate by mechanisms basically different from those of the pigeons.

Each homing experiment consists of two parts, the outward journey (managed by the experimenter) and the return flight (managed by the bird). It has to be proved, therefore, whether the second part not only succeeds the first, but also depends on it. Successful homing would entirely depend on information collected during the outward trip, if it were based on some kind of path integration (dead reckoning). The birds should measure then all their angular and linear motions, and with the resulting data they should continuously update an internal store that contains actual direction and distance to the home site where integration has started. Thus, the animal would carry its coordinate system with it. Non-recognized displacements would displace the whole system, and the animal would "home" to a fictitious goal accordingly displaced. Measurement of motion could be done without reference to external stimuli (idiothetically) and/or with reference to environmental cues (allothetically), preferably to directional cues like the sun or the geomagnetic field (Mittelstaedt, Mittelstaedt, 1973).

Path integration is known from several arthropods as, e.g., bees, ants, and spiders (v.Frisch, 1965; Wehner, 1982; Görner, 1966), but has also been shown in mice and walking geese over distances from less than a metre to a few hundreds or thousands of metres (Mittelstaedt, Mittelstaedt, 1982; v.Saint Paul, 1982). Longer-distance homing of passively displaced and afterwards free-flying pigeons, however, does not require path integration, as has been shown by severe disturbance or exclusion of potentially useful outward-journey stimuli (Wallraff, 1980b; Wallraff et al., 1980). (Some correlation between age and homeward directedness of initial bearings (Wiltschko, Wiltschko, 1982) does, of course, not imply evidence for path integration in pigeons, nor even for utilization of outward-journey information in general.)

An alternative mechanism of homing, which apparently is in fact utilized by birds, is some kind of site localization. In this case, the animal does not measure its movements, but deduces its momentary position in relation to home from site-dependent environmental features. The animal is thought to be provided with a "map" which in some way corresponds to these features. Two sorts of maps may be considered in this context (cf. Wallraff, 1974; Wiltschko, Wiltschko, 1978, 1982):

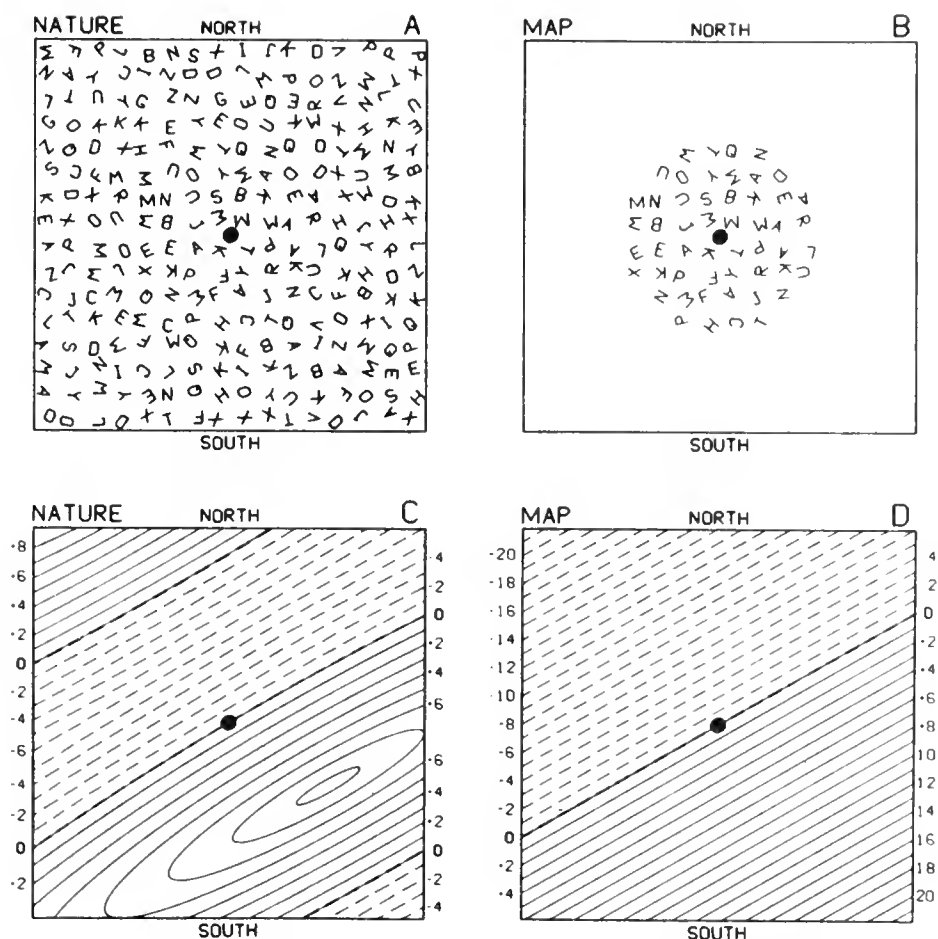


Fig. 2. A - a mosaic of individual landmarks, symbolized by letters, surrounding a bird's home site (central dot). B - the bird's corresponding mosaic map which is limited in extension in dependence of the bird's experience. C - iso-lines (arbitrary units) of a field of gradients surrounding a bird's home site. The line running through this site is designated as 0, higher values indicated by solid and lower values by broken lines. D - the bird's corresponding gradient map as established by extrapolation of home-site conditions. Notice that in C and D, for the sake of simplicity, only one coordinate is shown. For complete site localization, at least two sorts of gradient fields are required with the gradients intersecting at sufficiently large angles. The sections shown are thought to be of different size; sides of the square in A, B may be in the order of maximally a few hundred, those in C, D of a few thousand kilometres. Thus, the map area shown in B may roughly coincide in size with the central dot in C and D

The mosaic map represents many of the landmarks surrounding an animal's home in a similar way in which our maps show villages, forests, lakes, etc., possibly inclusive of their compass bearings with respect to home (Fig. 2A, B). Each tessera of the mosaic has its own quality and thus has to be learnt by individual experience. As a result, the range of the map is restricted to the area covered by the animal's activities or, due to remote sensing, to a somewhat more extended area.

The gradient map is based on physical parameters that quantitatively and systematically vary in space and thus form some fields of gradients being suited as coordinates for site localization. If an animal is informed on the directional alignment of at least two gradients and on the scalar values of the respective physical cues at the home site, it can, by extrapolation,

build up a map which is practically unlimited in its spatial extension (Fig. 2C,D). Its application, nevertheless, may be limited to a restricted range, if the environmental gradient fields are of less than global size. If, for instance, the distances between iso-lines in Fig. 2C,D corresponded to 100 km, the map would be perfectly correct within a radius of 600 km around home, and the signs of the differences against the home coordinate would coincide between nature and map up to more than 1000 km. Beyond some limit, however, the simple map would no longer fit the more complicated natural conditions.

Within their ranges of applicability, both kinds of maps provide a bird with information on its position in relation to home at any site irrespective of information picked up en-route to this site. This does not mean, however, that birds, even when using a map system, are not allowed to use en-route information. There are reasons to assume that homing pigeons permanently control their position whenever it is possible. Perception or measurement of the related environmental cues may not be possible equally well under all circumstances, and so the birds' decision on flight direction after a displacement may be influenced by stimuli actually perceived at the momentary location as well as by stimuli previously perceived during displacement. Site localizations during the outward journey are particularly useful, if the birds are transported to a site outside of the range within which they can make use of their map. Then their chances to reach this range are best if they follow a compass direction opposite to that toward which they had left it (cf. Wallraff et al., 1981; Ioalé et al., 1983).

A look at the literature (e.g., Wiltschko, Wiltschko, 1982) makes it necessary to emphasize that effects of some experimental treatment during the outward journey on subsequent initial orientation must not automatically be taken as an outcome of a path-integration mechanism being at work. If the treatment does not also affect homing success, or at least homing speed, it is even not allowed to conclude that information gathered during the outward journey is a necessary component of the navigational process, independently of whether such information might be involved in a path-integration or in a site-localization system. Effects on only initial orientation may simply reflect some transitory behavioural disturbance (see also Wallraff, 1980b).

There is little doubt that, at shorter distances, some pilotage by familiar landmarks and thus some mosaic system is involved. For homing over several hundreds of kilometres of unknown terrain, however, only utilization of more-or-less monotonic gradients appears conceivable. Theoretically, they could be used without a map, i.e. without knowledge of the compass alignment of respective gradients. The birds would only dispose then on the *x* and *y* values of their home coordinates and would have to scan the remote area by appropriate search flights in order to find the direction toward which the difference of actual *x* and *y* to these memorized values decreases. Obviously, however, pigeons do have a map that is linked to the compass scale (as indicated in Fig. 2D) and thus can immediately decide where to go when released at a distant site. This can be concluded from releases of birds with a

shifted sun compass (e.g., Keeton, 1974; Schmidt-Koenig, 1979; for extensive discussion see Wallraff, 1974) and results in the generally accepted two-step nature of homeward navigation: At first, the bird defines its position with respect to home on its "map", and then it realizes the deduced flight direction by means of its "compass" (map-and-compass concept of Kramer, 1953). The linkage between map and compass obviously occurs during the long-term exposure to the home-site conditions (Wallraff, 1974 and in prep.; see also Wiltschko et al., 1976; Wallraff, 1978). Even this calibration process and thus the development of a gradient map does not seem to require scanning of gradient fields by means of exercise flights in the home area, as the area of movements can be restricted to the few square metres of an aviary (e.g., Kramer, 1959; Wallraff, 1966, 1970, 1974).

In case of perfect coincidence between internal gradient map and external gradient fields, a bird would be able to steer the shortest course homeward from everywhere. With considerable probability, however, such perfect coincidence does not exist. Five possible sorts of discrepancies shall be enumerated (see also Wallraff, 1974). (1) The map underestimates or overestimates the steepness of the gradients, or it even includes only the signs of the slopes. (2) The map more-or-less misrepresents the compass alignments of the gradients. (3) The environmental gradient fields are less uniform as expected on the basis of a regular map. Non-uniformity may concern more-or-less local irregularities (anomalies) or the shape of the whole gradient field or gradient-field system (as schematically indicated in Fig. 2C). (4) Due to some noise in the related physical parameters and/or to some limitation in the accuracy of perception, the bird may not always be able to determine even the sign of the difference between a parameter actually measured at a remote site and the respective value at home. Thus, its map is too crude to work within a sub-threshold zone at shorter distances. (5) Momentarily or locally, a related parameter cannot be recognized at all and thus cannot be brought into relation with the map. (Simple example: sun navigation cannot be performed with the sun obscured by clouds, although clouds do not affect the sun's position.)

As a result of such discrepancies, the birds can scarcely be expected to fly the shortest way home from everywhere. Possible strategies to overcome resulting difficulties have been discussed earlier (Wallraff, 1974, 1980a). The fact that flight routes of homing pigeons commonly are more or less polarized toward a preferred compass direction, and thus show characteristic patterns involving systematic deviations from the shortest way home (e.g., Wallraff, 1974, 1978, 1982; Windsor, 1975), have been interpreted as an outcome of those strategies.

THE PHYSICAL SUBSTRATES FOR SITE LOCALIZATION

A mosaic map may be based on any detectable signals of the environment, may they be visual, acoustic, olfactory or whatsoever. A gradient map, in contrast, has to be based on particularly suited parameters which provide sufficiently large-scaled gradients. Consequently, search for potential navigational cues was nearly always focussed on those physical substrates

which were known to fulfill this precondition. Such substrates are very limited in number, however, and so attention has been concentrated to either astronomical cues (sun-navigation hypothesis; Matthews, 1953; Pennycuik, 1960) or, earlier as well as more recently, to the magnetic field of the earth (e.g., Yeagley, 1947; Walcott, 1982). Both features are, in principle, suited for site localization. Yet empirical research has ruled out sun navigation as a realistically possible basis of pigeon homing (e.g., Kramer, 1961; Keeton, 1974; Wallraff, 1974), and it has also shown that effective homing does not depend on undisturbed magnetic cues (e.g., Keeton, 1971; Walcott, 1977). Some spatial and temporal correlations (e.g., Keeton et al., 1974; Walcott, 1978, 1982; Kiepenheuer, 1982), though otherwise unexplained, cannot prove the magnetic field as a basis of the pigeons' map (cf. Wallraff, 1983). Nevertheless, magnetism seems to partake in one or the other way, but it remains doubtful whether it plays a central role in the process of site localization (Walcott, 1977; Visalberghi, Alleva, 1979; Wallraff, Foà, 1982).

While the deductive approach, starting from our knowledge about physical environmental features, has not been very successful thus far, it was a fortunate event when Papi et al. (1971, 1972) were able to open an unexpected inductive way. Before that, nobody could imagine that olfaction might play a substantial role in long-distance navigation, and even Papi (1976) considered only an olfactory mosaic system. Further experimental data, however, which demonstrated an intact olfactory apparatus being a necessary precondition for homeward orientation over distances up to 500 km and more (Wallraff, 1981; Ioalé et al., 1983; see also Papi, 1982), can hardly be explained without assuming a large-scale gradient system of odorous substances (Wallraff, 1980c). Although nothing like this is presently known, its existence cannot a priori be excluded.

SUMMARY

Migratory orientation appears primarily based on compass mechanisms in which the geomagnetic field as well as astronomical cues are involved. The distances covered may indirectly result from an endogenous temporal program. Goal-oriented navigation takes certainly part as soon as a goal area has been experienced. Homing from remote sites after passive displacement (mostly conducted with homing pigeons) is concluded to be based on some method of site localization and not on path integration. Within a limited area around home, site localization may be performed by use of a 'mosaic map', but over longer distances some sort of a 'gradient map' (bicoordinate navigation) is most likely to be utilized. At least substantial parts of the physical substrates constituting the assumed gradient fields appear to consist of atmospheric odours, whereas the role of the geomagnetic field seems to be comparatively subordinate in this context.

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THE CONTRIBUTION OF RADAR AND VISUAL TECHNIQUES TO ORIENTATION RESEARCH

Kenneth P. Able

Department of Biological Sciences State University of New York,
Albany, New York, USA

Recent years have seen an emphasis on studies of migratory orientation in caged birds. This research (see the review by Wiltschko in this volume), has revealed new orientation cues used by migratory birds as well as relationships among known sources of directional information. However, we should be interested in the actions of a bird in an orientation cage only to the extent that they reflect the migratory behavior of the same bird under natural conditions. Radar and techniques of visual observation, biased though they often are, provide our only window on the world of nocturnal bird migration. Therefore, data obtained by these methods provide the background against which we must evaluate our experimental procedures and results; ideally, they should also be the foundation upon which experimental investigations are built. Some of the recent discoveries described herein could not have been predicted from nor observed in controlled experiments. The examples I have selected illustrate the complex interactions between bird and environment that characterize migratory orientation in free flight.

DIRECTIONAL DECISION-MAKING BY FREE-FLYING NOCTURNAL MIGRANTS

Radar observations of oriented migratory flight under solid overcast skies were in part responsible for the development of the notion that birds must be using several independent cues in orientation. Experiments with migrants in orientation cages have confirmed this notion. Recent field work has generated a considerable amount of information on the relationships among these various sources of directional information.

Orientation cage studies have shown that migratory orientation during twilight is at least sometimes based on the sun (Moore, 1980, 1982) and skylight polarization patterns (Able, 1982a). Radar data have produced a rather similar picture. Emlen and Demong (1978) released and tracked White-throated Sparrows (Zonotrichia albicollis) during early twilight at Wallops Island, Virginia. The sparrows headed in an appropriate northward spring direction, presumably based on the glow of sunset in the western sky. At the same locality, during a prolonged period of continuous solid overcast, the orientation of wild migrants deteriorated. A break in the clouds late in the afternoon of the third day of continuous overcast afforded a view of the sun and sunset. On that night, orientation was dramatically improved, but deteriorated during the next two days as overcast solidified again (Emlen, 1980).

Studies with tracking radar near Albany, New York, have revealed complex relationships among celestial cues and wind direction (Able, 1978, 1982b). I have tracked wild migrants on nights when winds were opposed to the normal direction of migration for the season. When birds had a view of sunset or stars they oriented in the expected direction for the season. When solid cloud cover prevented them from seeing the sun in the late afternoon or the stars at night, they headed downwind and thus moved in an inappropriate di-

rection for the season. The pattern clearly points to primacy of celestial cues over wind direction in this region and suggests that either sun related cues or stars are sufficient to allow birds to make an appropriate directional decision. In the absence of these visual cues, they rely on wind direction. We have explored this relationship further by releasing White-throated Sparrows from balloon-borne boxes as described by Demong and Emlen (1978). All releases were performed after dark on clear nights with winds opposed to the normal seasonal migration direction. We released two types of birds: normal, unaltered sparrows and sparrows fitted with frosted lenses that prevented any detailed form vision. As we had predicted from the pattern observed among wild migrants, the birds without lenses headed primarily in the directions expected of White-throated Sparrows at this locality, but the birds wearing lenses headed downwind (see Able et al., 1982 for details). It is remarkable that birds with drastically reduced vision could determine the wind direction even crudely while flying. Larkin (1980) has obtained evidence that birds flying over open ocean at night are also responsive to wind direction, but the mechanism by which they assess it remains mysterious.

Reversed migrations and other movements in seemingly inappropriate directions have been observed in every area where any significant amount of radar or visual observation has been made. Nearly all studies agree that such flights generally take place with a following wind, i.e., when winds are opposed to the usual flow of migration at that season. My observations, described above, show that reversed migrations are also more likely to occur under solid overcast skies and a similar trend has been noted by Bruderer (1978) and Richardson (1982).

Once a directional decision has been made and birds are aloft, the presence of solid cloud cover seems to have remarkably little effect on their orientation. Indeed, one of the most enduring generalizations from radar and visual studies is that random flight directions or tracks of apparently disoriented birds are virtually never observed. A priori we might expect at least some slight impairment in the ability of birds to maintain a given orientation direction, especially if celestial cues are important in this process, as suggested by the cage studies of Wiltschko and Wiltschko (1978). I have recently analyzed a series of tracks of migrants flying under solid overcast and compared them with a set of tracks obtained under clear skies and matched as closely as possible in terms of date, wind direction, flight altitude, time of night, etc. (Able, 1982c). The tracks of the birds flying under solid overcast were as straight and level as those under clear skies and birds flew at similar air speeds. The dispersion among tracks on a given night was not consistently greater under overcast than under clear skies (contrary to the statement in Able, 1980a, based on a preliminary analysis).

The only marked effect of overcast on orientation occurred on nights when the altitudes of the birds tracked indicated that they were flying within clouds or between opaque cloud layers. On each of four such nights, the headings of the birds were not oriented and their tracks were significantly less linear than those of birds flying beneath solid cloud cover. The random orientation among the population of birds aloft probably resulted from the accumulation of errors in maintaining an exact heading. However, it

seems clear from Griffin's (1973) tracking studies of birds flying inside clouds that disorientation need not always occur; indeed his birds were usually moving in the normal seasonal directions.

The picture that has emerged from the relatively few documented cases of orientation under long-term solid overcast is also somewhat inconsistent. The case described by Emlen (1980) suggested that the absence of celestial cues for about 24 h was sufficient to lead to disorientation among wild migrants, and Steidinger (1968) found increased scatter among migrants departing under cloud layers of several days' duration. The two cases I have examined (Able, 1982c) had random headings only on those nights when birds appeared to be inside clouds. Clearly, the number of cases is too few to warrant generalizations, but it appears that long-term overcast by itself does not necessarily result in disorientation among migrating birds. In the future, more careful attention needs to be paid to the altitudes of both birds and clouds.

One thing that does seem to clearly emerge from the observation of migrants under overcast skies is that whatever role celestial cues normally play in the selection and maintenance of headings, alternate and equally effective means apparently exist. Orientation cage studies strongly suggest the magnetic compass as a primary candidate. Unfortunately, field observations of free-flying migrants have failed to produce any evidence of a directional magnetic effect; only an increase in dispersion of track directions with increasing intensity of natural magnetic disturbance has been reported by Moore (1977). The lack of clear evidence of magnetic involvement in the orientation cage studies and field observations.

IN-FLIGHT ADJUSTMENTS OF ORIENTATION

Detailed observations of nocturnal migrants enroute have shown that birds do not simply choose a direction and maintain it mechanically. On the contrary, birds aloft appear to respond in complex ways to the environment around them and to the air through which they are moving, performing a variety of adjustments in their behavior, including orientation.

The early years of radar observation gave rise to a consensus that flight directions of night migrants seemed to be influenced very little by topographic features or other cues on the ground. When I last reviewed this area (Able, 1980a), I noted a few exceptions to that general rule and suggested that landmarks might turn out to be important in more subtle ways such as gauging or correcting for wind drift. Alerstam and Pettersson (1976) had shown that several species of birds migrating across the Baltic Sea seemed to use waves in an attempt to compensate for wind drift, treating them as stationary landmarks and thus drifting with the moving waves. Since that was written, new data have appeared.

Songbirds migrating at night over inland areas of northeastern North America seem often to be drifted by cross-winds (Able, 1974a; Richardson, 1982). On calm nights the mean flight direction is southwest; thus the strong northwest and west winds that occur following the passage of a cold front have considerable potential to produce lateral drift. Bingman et al. (1982) made simultaneous observations of nocturnal migration at three sites in New York, two in upland areas devoid of conspicuous landmarks, the third adjacent to the Hudson River which flows north-south and is flanked by lights on build-

ings, along highways, etc. In all winds except those from the northwest-west at > 5 m/s, birds flew mostly southwest at all sites and there were no differences in direction among them. In winds from northwest-west, however, birds away from the river moved south-southeast whereas those in the vicinity of the river flew south-southwest parallel to its course. The change in direction was accompanied by a relative increase in the traffic rate of migrants along the river, as one would expect if drifting birds were turning upon reaching this conspicuous linear landmark. The data are thus consistent with the hypothesis that the birds were compensating at least partially for the drift accrued while flying over more featureless terrain.

In the more dramatic landscape of Switzerland, Bruderer and his colleagues have also found selective influences of landmarks upon orientation (Rüsch, Bruderer, 1981; Bruderer, 1982). Birds flying over rugged terrain in the Alps under totally overcast skies were influenced by topographic features, regardless of wind direction. Under both cloudy and clear skies, birds migrating in west winds (potentially drifting in this region where the main direction of migration is southwest) responded to local topographical leading lines in a manner that compensated for wind drift.

The generalization that passerine nocturnal migrants usually pass over coastlines, islands, river valleys and mountain ridges without changing course remains true. Diurnal migrants are much more likely to respond to such features. However, it is now becoming clear that night migrants do respond to landmarks, but in a facultative manner. It is thus easy to understand why field studies that searched for constant influences of topographic features failed to find them.

Likewise, it has become increasingly apparent that there will be no simple answer to the wind drift question. It is premature to attempt any firm generalizations, but it appears that birds migrating in coastal areas often compensate completely for drift whereas over inland areas and open ocean they more often incur drift. Variability is to be expected as individual birds play out different migration strategies. Alerstam (1981) has outlined circumstances in which it might be advantageous for migrants to allow themselves to be drifted. Williams and Williams (1978) have explored one such situation, the trans-Atlantic migration of birds from North to South America. Movements made up of both waders and passerines depart from New England and the Maritime Provinces of Canada on northwesterly and westerly post-frontal winds. Data from shipboard and land-based radars throughout the western Atlantic showed that the birds maintained a constant southeastward heading throughout this vast journey, first drifting eastward far out over the ocean, then westward on the easterly trade winds into the continent.

Additional complexity in the flight behavior of night migrants has been described by Larkin and Thompson (1980). In analyzing a large sample of radar tracks they noticed that even within a single night the pool of migrants consisted of two populations: birds that had faster air speeds (> 8 m/s) and those with remarkably slow speeds (< 8 m/s). There were good reasons to believe that most of these very slow targets were in fact birds. The slowly flying targets could also be characterized in another way: as a group they tended to be poorly oriented or to head in the opposite direction from faster

flying individuals in the same season or even in the same night. Sometimes they tended to fly at lower altitudes and they were relatively more numerous on nights with seasonally unfavorable winds. What these unique results mean is not yet clear, but they certainly suggest that the migrants aloft on a given night are anything but a homogeneous population and individuals that initiate reversed migration or orient in inappropriate directions may be a highly biased sample in ways as yet unknown.

REORIENTATION FOLLOWING NOCTURNAL MIGRATION

The evidence that experienced migrants of many species return year after year to specific sites on both wintering and breeding grounds is unequivocal. On the other hand, attempts to observe goal oriented behavior in free-flying migrants or to elicit it in caged birds have been largely unsuccessful. Yet during the course of migration, birds are often displaced by winds or otherwise find themselves off the normal route. Many of these birds, including many immatures on their first autumn migration, make compensatory flights, especially in coastal and offshore areas (see Able, 1980b). Such behavior does not necessarily imply a goal-oriented response and because at least some immature birds perform these flights, a more reasonable interpretation is probably that they involve a compass-based response to wind drift accrued and monitored during a previous nocturnal flight. These reoriented flights occur primarily in the early morning hours and are particularly common in coastal areas (e.g., Baird, Nisbet, 1960; Myres, 1964; DeSante, 1973; Richardson, 1978). There they might represent either a response triggered in a bird finding itself over water at dawn or a search for more favorable habitat, as suggested by Alerstam (1978). That, however, cannot be the whole story.

In inland South Carolina, Gauthreaux (1978) has studied similar morning flights of typical nocturnal migrants. These movements are apparently initiated by birds on the ground, i.e., they are not simply uninterrupted continuations of the previous night's migration. The birds are often flocked and there is frequent calling which often seems to stimulate birds on the ground to take off and join the flock. Like the reoriented flights of migrants in offshore and coastal areas of eastern North America, the predominant direction of movement in South Carolina is toward northwest, the expected direction if birds were correcting for drift by westerly winds. Occasionally, Gauthreaux has seen morning flights toward southeast which appeared to be correlated with the occurrence of easterly winds on previous nights. It seems likely that these morning flights involve compensation for displacement in some way, but again they do not necessarily imply true navigation.

Flights of typical nocturnal migrants in the early morning can be seen in many areas of North America, at least, but systematic observations have been made in only one other locality, upstate New York (Bingman, 1980). The behavior of the birds was in every way similar to that observed by Gauthreaux in South Carolina except that the flights were not reoriented. In both spring and fall the direction of morning flight was generally similar to that during the preceding night. Why this difference should exist is not clear, but it may relate to other regional variations in orientation behavior. Night migrants in northeastern North America are surely drifted by lateral wind compo-

nents on some nights (Able, 1974a; Richardson, 1982), but in the southeastern United States downwind flight is a common occurrence (Able, 1974b). This difference may result in birds in the southeastern United States being displaced greater distances by wind, and compensation via morning flight may consequently be more frequent.

FUTURE OF RADAR AND VISUAL STUDIES

It is obvious that observations of free-flying migrants by radar and visual methods continue to provide new insights into orientation behavior. Field observations cannot substitute for carefully controlled experiments. On the other hand, the complex strategies revealed by radar and visual studies warn us that we will develop a very incomplete picture if we rely too heavily on studies of birds in orientation cages.

The early years of "radar ornithology" were characterized by broad-scale regional surveys, employing long-range radars to make observations over all seasons for several years. To a large degree, this type of study has been replaced by research employing smaller, shorter range tracking radars. Simultaneously, there has been a decrease in purely descriptive work and an increase in the use of these methods to answer specific questions. In terms of learning new things about orientation, this is a more efficient approach. Used in this selective manner and combined wherever possible with experimental manipulations, radar and direct visual methods of observing bird migration should for some time continue to provide new and important insights into the unresolved problems of migratory orientation and navigation.

SUMMARY

Radar and visual methods of observing nocturnal bird migration continue to provide new and important insights into unresolved problems of migratory orientation and navigation. Recent radar studies have provided data on the role of the sun in directional decision-making by nocturnal migrants. Flying birds are able to determine wind direction with remarkable precision and use it as an orientation cue under certain conditions. Overcast skies increase the likelihood that birds will perform downwind flights in reversed or other peculiar directions. Otherwise, except when flying inside clouds, overcast has little effect on birds' orientation. To date, field studies have failed to reveal any evidence of major magnetic influences on orientation. Migrants enroute seem to employ a complex array of strategies, sometimes being drifted by wind, sometimes correcting for drift by using landmarks at night.

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THE ROLE OF ARTIFICIAL LIGHT SOURCES FOR THE VISUAL
ORIENTATION OF EUROPEAN ROBINS (ERITHACUS RUBECULA)

E. Vilks, Y. Katz, V. Liepa

Institute of Biology of the Latvian SSR Academy of Sciences, Riga, USSR

A large series of experiments (over 4000 bird-nights) with European Robin orientation was carried out at the Laboratory of Ornithology of Institute of Biology of the Latvian Academy of Sciences, beginning in 1966.

For the study of significance and interaction of stellar and magnetic information at the selection and maintenance of direction by Robins in round cages a special planetarium was built, in which it was possible to shift the angle between the stellar and magnetic meridian in relation to the geographical one. Seven combinations of various directions of stellar and magnetic meridians were used. In control experiments both the stellar and magnetic meridian coincided with the geographical one. It appeared that at any combination of stellar and magnetic meridian direction the orientation of Robins was determined by the planetarium stellar pattern only (Fig.1). The reaction of Robins to the shifting of stellar or magnetic meridian during the course of an experiment was also studied by comparing the orientation of birds before and after the shift. In that case the shift of stellar meridian caused a change in the Robins' orientation by a corresponding angle (Tabl.1). On the contrary, by shifting of magnetic meridian in course of an experiment the birds maintained the previous direction of movement.

Robins exposed to a rotating planetarium sky shifted their orientation during the night. We found a strong dependence of direction of movements of birds in round cages on the rotation and decline angles of the axis of stellar sphere (Katz, Vilks, 1979). It appeared that the Robins moved in the direction of the vector of the distribution of illumination produced by the stellar pattern. This vector, in nightly and seasonal mean value, was close to the migratory direction of Robins (Katz, Vilks, 1981). Yet at separate hours of the night the gradual changes in preferred directions according to the illumination vector were rather considerable. Such a regularity was shown by testing birds under planetarium stars with the Milky Way, as well as under stars only and the Milky Way only (Fig.2). Because the Milky Way in the planetarium is produced by means of separate projector in the shape of a diffuse stripe on the dome, this stripe and the pattern of artificial stars in shape of separate light dots look completely different. Yet referring to general distribution of light dots or brightness of diffuse sectors of Milky Way on the dome of the planetarium both these models of astronomical cues follow the same regularities, because they both reflect real distribution in both models almost coincide.

It should be emphasized that the birds oriented themselves exactly in the direction of the mean vector of the light distribution, which did not always coincide with the brightest visible sector of the celestial sphere. Obviously Robins tended to move not always in the direction of the lightest side, but also took into account the entire circular distribution of illumination.

The light-vectorial nature of orientation of Robins in a planetarium was confirmed by experiments in which an arbitrary pattern of light spots with a

known light distribution vector was projected on the planetarium dome.

The direction of the Robins' movements in the planetarium was not determined by the physiological state of the birds according to season, but only by the projected stellar pattern.

The above-mentioned features of Robins' orientation were observed by us in three planetariums with the aid of two different stellar projectors (Katz, Vilks, 1979).

Fig.1. Orientation of European Robins in planetarium by various combinations of directions of stellar and magnetic meridian

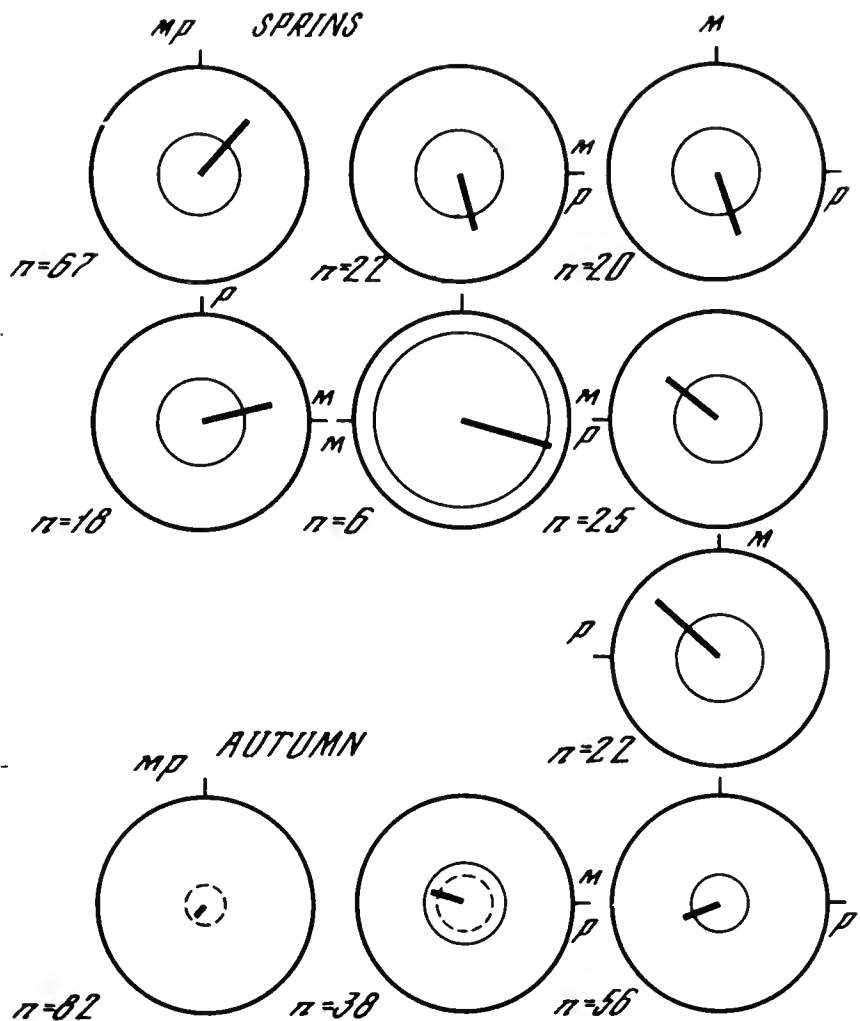


Table 1. Orientation changes of Robins after the shift of stellar or magnetic meridian (+ Clockwise shift)

| Shift, direction of meridian | Shift of magnetic meridian | | | Shift of stellar meridian | | |
|------------------------------|----------------------------|------|------|---------------------------|------|------|
| | n | a | r | n | a | r |
| N → E (+90°) | 68 | +2° | 0.75 | 66 | +84° | 0.42 |
| E → N (-90°) | 24 | +10° | 0.87 | 57 | -86° | 0.57 |
| N → W (-90°) | 19 | +7° | 0.86 | 34 | -85° | 0.85 |
| W → N (+90°) | 6 | +23 | 0.89 | 17 | +82° | 0.56 |

The analysis of published data of other authors show that a majority of research works, carried out with round cages under the planetarium or natural sky, also showed a gradual shift of preferred directions, which can be the result of light-vectorial orientation (Fig.3) - (Sauer, 1957; Hamilton, 1962; Mewaldt et al., 1964; Emlen, 1967; Rabøl, 1972; Wiltschko, Wiltschko, 1974, 1975 etc.). The authors of these works usually give another explanation for such facts, or do not take them into consideration at all.

Consequently, the tendency of birds to move in the direction of the light-vector is a rather widespread phenomenon. It remains to be determined whether such a reaction has any essential significance in the biological mechanism of orientation of birds. On the one hand, it is difficult to believe that such astonishing capabilities of birds could be without importance in the complex of spatial orientation. On the other hand, in terms of night migration of natural conditions, orientation by continually changing azimuth with the vector of light distribution in the stellar pattern would cause the birds to continually change migratory direction, which would not lead them to the goal of migration.

Apart from planetarium experiments in our laboratory, the work was also

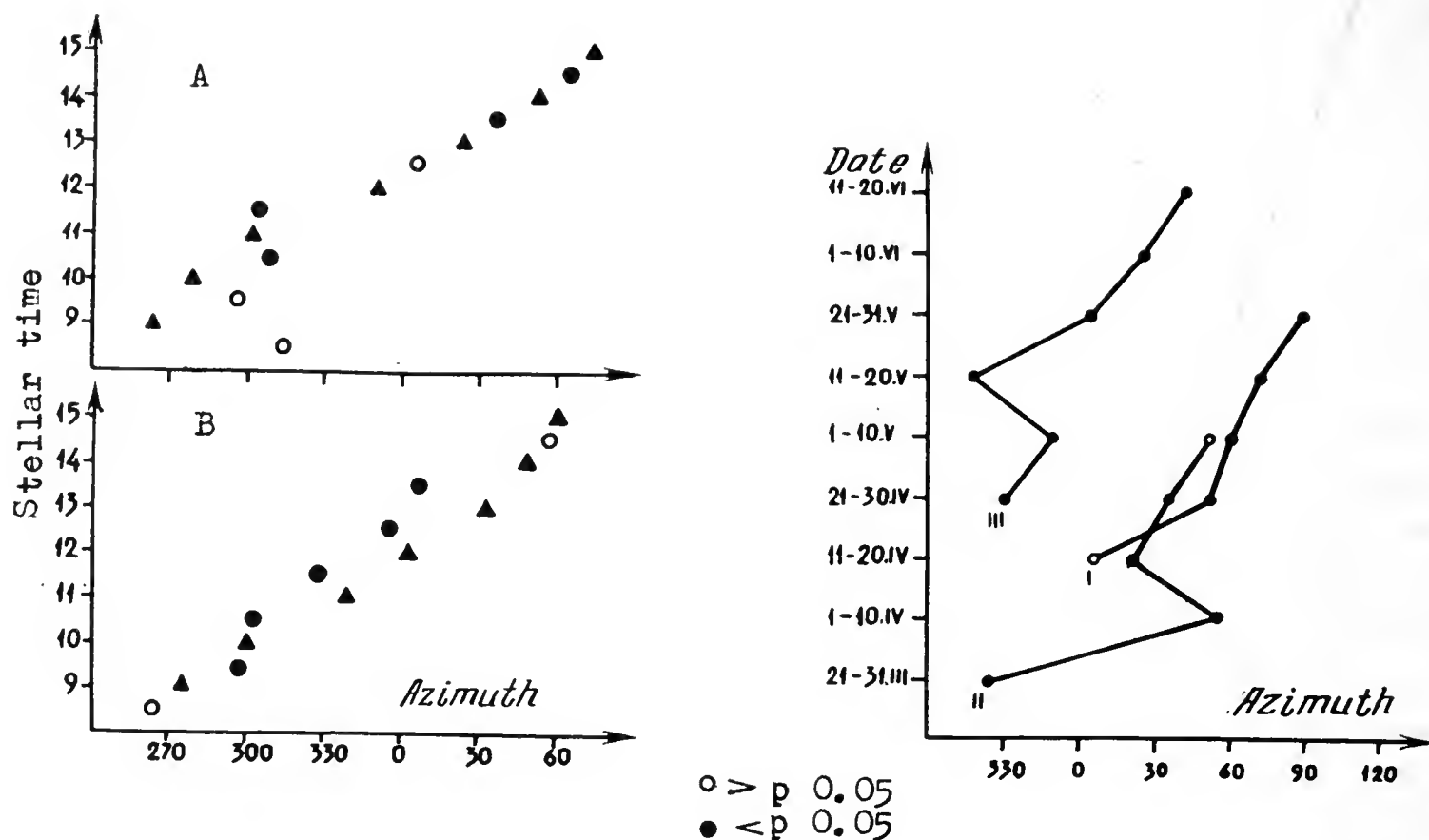


Fig. 2. Orientation of Robins (dots) and direction of vector of light-distribution (triangles). A-milky way only; B-stars without milky

Fig. 3. Shift of bird orientation during spring experiment under stellar sky. I - Katz, Vilks (1979); II - W. Wiltschko, R. Wiltschko (1974, 1975); III - Mewaldt et al. (1964)

carried out in another direction - the orientation of Robins in round cages, placed in closed chambers with presentation of a single light cue (small light spots) was studied. In general the experiments were carried out in two versions - by the light cue switched on at the time of sunset and at 22:00 hours local time. When the light spot was switched on at the instant of sunset, the initial movements of birds were directed to the left of the artificial cue. When the light spot was turned on later, the initial directions became more scattered and when the cue appeared at the 5-6th hour of the experiment, they were random. Nevertheless, the concentration of movements of individual birds under these circumstances remained high. At the end of night, preferred directions of Robins were concentrated close to the opposite side from the artificial light cue. The transition from the evening to the morning direction in general occurred in two ways: by way of gradual shifting or a rapid leap after continuous maintenance of evening orientation. The latter case was typical for birds, juveniles as well as adults, who were prevented from seeing the natural sky from midsummer till initiation of the migrational season. Most of the visually experienced birds under similar conditions showed a compensation type shifting of preferred directions in relation to the light spot.

One of authors of this report (V. Liepa) explains part of these reactions as expression of time compensated stellar-compass orientation (Liepa, 1978). The rates of orientation shift differed among the birds in autumn depending upon their initial angle of movements in relation to the single light spot, turned on at 22:00. It was supposed, that this angle corresponds to the angle

between the choosed direction of the bird and his critical stellar cue in night sky. Hence the azimuths of hypothestical stellar cues for birds with different initial angles of movement were calculated for the moment of appearance of the light spot. As the height of critical cues for all birds was assumed the height of Polaris (57°), because one of our groups of birds displayed a constant angle orientation to the light spot. According to the initial azimuth and height of hypothetical stellar cues the theoretical curves of compensation for thir movements during the remaining part of night was constructed. The best correspondence of shifting rates of preferred directions of our birds with theoretical curves of compensation for their critical stellar cues was found supposing that the birds tend to move south, not southwest - the standart direction of migration for this species. These results are interpreted by V.Liepa as an indication, that under certain circumstances the Robins are able to realize the selection and maintenance of the direction from individual stellar cues. In favour of that, according to V.Liepa is also the fact that the rhythms of light compass orientation of Robins are individually specific.

Another author of our report (Y.Katz) explains this behaviour by the ability of Robins to perform sun-compass orientation. As proofs he uses the following facts. The movements of birds in relation to an artificial cue at the instant of sunset and sunrise correspond to the choice of the migratory direction on the basis of a fixed angle in relation to the sun. Gradual change of direction of movements in the course of a night corresponds with the maintenance of a chosen direction with the aid of sun.

The direction of movements of birds in relation to an artificial cue at the instant of sunset remain constant over the course of a season. This may be taken as an indication of the existence of a fixed azimuth of migration, chosen at the start in relation to the setting sun. The existence of such a given, maybe inherited azimuth of migration is also observed in birds, kept a long time in visual isolation from astronomical cues.

According to third author of this report (E.Vilks), the hypotesis of Y.Katz better explains all the facts observed in course of our experiments. Also this hypothesis accords better with the observed features of bird migration in natural conditions.

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INTERACTION OF DIFFERENT ORIENTATION CUES

W.Wiltschko, R.Wiltschko

Department of Zoology, J.W.Goethe-University,

Frankfurt a.M., FRG

INTRODUCTION

Bird orientation has been found to be a highly complex process where a variety of environmental factors combine to produce the observed behavioral output. Many of these cues have proven to supply redundant information while others play a role only in certain situations. In spite of the intensive research in this field, our knowledge of the interrelation of the various cues is still rather incomplete. Certain ideas, however, appear correct: Although some factors seem to be used by all birds, there is no general hierarchy of cues; the significance of the individual cues depends strongly on a given situation. In particular, there seems to be a general tendency that simple, basic cues are later supplemented by other information. Some factors are very important during the ontogeny of the orientation system, but later they are replaced in part by more complex learned mechanisms. - In the present paper we will give two examples of such a developmental sequence: the orientation of night-migrating birds and the sun compass orientation of homing pigeons.

THE ORIENTATION OF NIGHT-MIGRATING BIRDS

Stars, magnetic field, celestial rotation, wind, sun set point, sky light distribution, polarized light and prominent topographic features have been shown to influence the directions of nocturnal migrants. The experiments demonstrating the effects of the various types of cues have been carried out using different test species; so we do not know whether these factors affect all bird species alike. Nevertheless, we will generalize and try to outline a picture of their interaction which must, of course remain speculative in many respects.

Young birds on their first migration transfer the genetically encoded information about their migratory direction into an actual flight direction. The factors functioning as a reference system for this information must provide a compass in the sense that they distinguish directions in space. Two such systems will be discussed here: celestial rotation and the magnetic field, i.e. a migratory direction "south" may be encoded as "away from the center of celestial rotation" and/or as "toward the magnetic equator" (since the birds' magnetic compass does not distinguish "north" and "south", but "poleward" and "equatorward", comp. Wiltschko, 1980).

A role of celestial rotation as a reference for the migratory direction was first suggested by Emlen's (1970) planetarium experiments with Indigo Buntings, Passerina cyanea. He handraised young birds under a "sky" which was rotating around Beteigeuze in Orion. When in the following autumn season these birds were tested under a stationary planetarium sky, they oriented away from the former center of rotation just as controls moved away from the

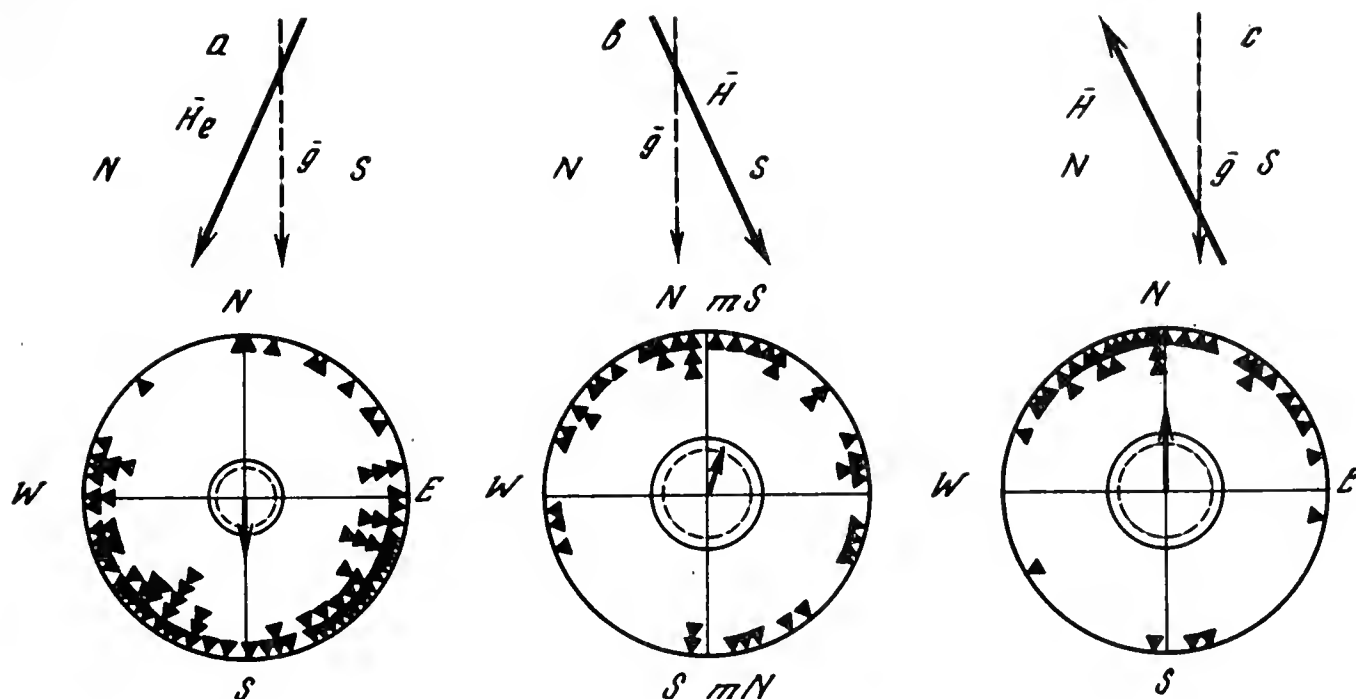


Fig. 1. Pied Flycatchers, handraised without ever seeing the sky are able to localize their migratory direction during their first autumn migration using a magnetic "inclination compass". a - geomagnetic field, b - horizontal component reversed, c - vertical component reversed.

Upper diagrams: vertical section through the magnetic field indicating the position of the magnetic field vectors in space. H_e - geomagnetic field vector at the test location, H - experimental magnetic field vector, g - gravity vector. Lower diagrams: orientation behaviour of handraised Pied Flycatchers in autumn. Each triangle marks the heading of an individual bird during one test night; the mean vector of the sample is represented by the arrow with its length drawn proportional to the radius of the circle = 1. The two inner circles represent the 5% (dotted) and the 1% significance border of the Rayleigh Test (Batschelet, 1965). Data from Beck, Wiltschko (1982)

north star, i.e. the birds had established a star compass, calibrating certain star patterns in relation to the night sky's center of rotation. Emlen assumes that this process took place between fledging and the beginning of migration. - Recently, similar results were obtained with Garden Warblers, Sylvia borin: Birds handraised under a rotating artificial "sky" oriented "southward" with respect to the former center of rotation when they were tested under the same, now stationary "sky" in the absence of meaningful magnetic information (see Fig. 2a, Wiltschko, 1982).

The magnetic field appears to be an even more suitable reference system for innate directional information for it can be used directly to localize a migratory direction. Young Garden Warblers and Pied Flycatchers, Ficedula hypoleuca, that had been handraised without ever seeing the sky showed directional tendencies coinciding with the migratory direction of their free flying conspecifics (Gwinner, Wiltschko, 1978), and they changed their directional preferences accordingly when the magnetic field was altered (Fig. 1; Beck, Wiltschko, 1982).

While celestial rotation and the magnetic field serve as reference systems for an innate migratory direction, many more cues are involved in the actual

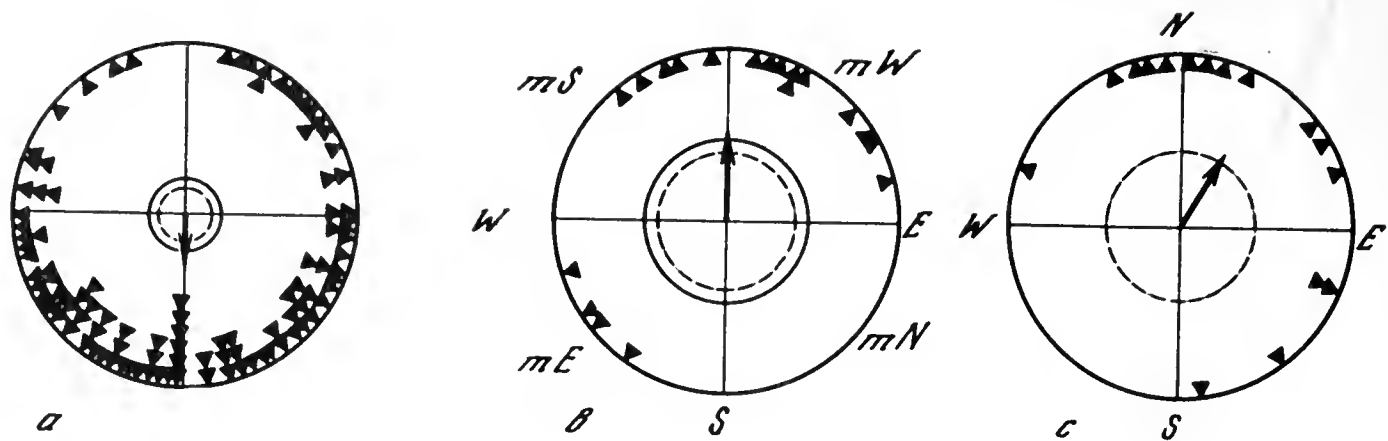


Fig. 2. Autumn experiments show that in Garden Warblers the directional information of the stars can be derived from celestial rotation as well as from the magnetic field

a - tested under artificial stars in the absence of meaningful magnetic information, young handraised birds oriented away from the former center of rotation experienced during rearing. - Data from Fergenbauer et al., in prep.; see W.Wiltschko (1982). b - tested under the natural stars in an altered magnetic field (mN indicates the position of experimental magnetic north in geographic ESE) birds trapped during migration selected their migratory direction according to experimental magnetic north in spite of contradictory information from the stars (mean of the control = 239° SW, not shown). c - in later tests under the natural stars in the absence of meaningful magnetic information the same birds continued in the same direction. (b) and (c): data from W.Wiltschko, R.Wiltschko (1975a). a, c - magnetic field reduced, b - magnetic north experimentally turned to 120° ESE. Meaning of symbols as in Fig.1

process of determining the flight direction on a given night. The most prominent are the stars. Orientation appeared to be so much better and more accurate when stars were visible (for summary, see Wallraff, 1972) that the magnetic compass was looked upon as only a subsidiary mechanism on overcast nights. This conclusion was supported by cage experiments where the stars and the magnetic field gave contradictory information; in such a test condition, Indigo Buntings seemed to follow the stars (Emlen, 1967). Similar results were obtained for European Robins, *Erithacus rubecula*, by Katz, Vilks (1979), whose findings also emphasize the importance of celestial rotation. They observed a certain hourly shift in the directional tendencies of their test birds, and they concluded that the overall vector of sky illumination rather than star patterns was used (Katz, Vilks, 1981).

In outdoor experiments where magnetic north was experimentally altered, European Robins at first appeared to disregard the magnetic information and continued toward their normal migratory direction. After a few days, however, the birds changed their behavior and selected their migratory direction relative to experimental magnetic north, this inspite of contradicting information from the natural stars. Tested without meaningful magnetic information they now continued in the same direction by the stars alone thus indicating that they had recalibrated their star compass by the experimental magnetic

field (Wiltschko, Wiltschko, 1975b). Several species of European Warblers, genus Sylvia, seemed to react much faster to a change in magnetic north (Wiltschko, Wiltschko, 1975a). Among them was the Garden Warbler, a species that had been shown to orient away from the center of celestial rotation (see above). Apparently these birds establish a star compass calibrated by celestial rotation during their upbringing, which, during actual migration, is controlled and recalibrated by the magnetic field (Fig.2; comp. Wiltschko, 1982). - The matter is further complicated by the finding that seeing the stars during upbringing seems to affect the birds' orientation by the magnetic field. When tested without visual cues, Garden Warblers that had been prevented from seeing the sky during ontogeny oriented much better than birds that had been brought up seeing the sun and the stars (Wiltschko et al., 1980). Bingman (1981) also reported that during ontogeny experience with the sky affected the magnetic orientation of handraised Savannah Sparrows, Passerculus sandwichensis. Since most nocturnal migrants start their flights at dusk, the sun set point has also been suggested to play a role in the orientation of night migrating birds (e.g., Vleugel, 1953), an assumption that has been supported by several radar studies (e.g., Emlen, Demong, 1978) and by cage experiments with Savannah Sparrows (Moore, 1978) and Whitethroated Sparrows, Zonotrichia albicollis (Bingman, Able, 1979). Skylight polarization may also be used at sunset (Able, 1982). - Because the geographic position of sun set varies considerably with latitude and with season, it became an interesting question whether sun set represents a cue of innate significance or whether it is merely a derived cue calibrated by some other compass. Experiments with handraised birds suggest the latter. Young European Robins showed the normally observed shift to sun set only when they had experienced the natural sky during their upbringing (Katz, 1980). Young Savannah Sparrows needed information from the magnetic field in order to orient at sun set, while for adult birds, sun set alone proved sufficient (Bingman, 1981). In summary, sun set appears to be a learned cue, and its use may parallel the use of the stars.

Aside from these cues that provide directional information, a variety of other factors like wind, meteorological factors, topographic features etc. have been found to influence nocturnal bird migration. The large amount of literature describing their effects cannot be summarized in this paper (see Alerstam, 1976; Bruderer, 1977, 1982; Able, 1980), here we will only state that they seem to be used mainly to facilitate maintaining a straight course and/or to help the birds find optimal conditions for their migration.

All the findings discussed here, even if some of them still appear to be somewhat contradictory, point out that the migrants' orientation system is highly flexible. Starting from fairly simple reference systems of genetically encoded directional information, a multitude of cues can be incorporated via learning processes. The primary sources of directional information, like celestial rotation and the magnetic field, play an extremely important role in early calibration of other cues, while during actual migration, their role is far less obvious. The magnetic field still seems to be used as an underlying reference system against which the other systems are controlled, and it may act as a back-up system on overcast nights. A flight direction on a given

night, however, might be determined by stars, sky light distribution and sun set, with meteorological and topographical information also affecting the birds' decisions.

COMPASS ORIENTATION OF HOMING PIGEONS

The development of compass orientation in young homing pigeons in a well studied example of the changing role of cues during ontogeny. - When the young pigeons become able to fly, their only means of directional orientation appears to be a magnetic compass provided by their ability to perceive the magnetic field. This is indicated by experiments in which pigeons were released carrying small magnets thus disrupting their magnetic compass: Flying under sun, young, inexperienced birds were disoriented when experienced pigeons were unaffected. The latter were apparently making use of their sun compass (Keeton, 1971).

The dominant role of the sun compass in the orientation of old, experienced pigeons has been documented by numerous clock-shift experiments (Schmidt-Koenig, 1961; for summary, see R. Wiltschko, 1980): If pigeons' internal clock is phase-shifted 6 h slow and then the birds are released under the sun at noon, their subjective "morning", they interpret the noon sun in the south to be the morning sun in the east resulting in their vanishing bearings deviating approximately 90° clockwise of those of untreated controls (Fig. 3, a,b). A corresponding counterclockwise deviation results if the birds are shifted 6 h fast. Such deviations indicate that they use the sun to localize their home direction, compensating for its constantly changing azimuth by means of their internal clock.

Very young, inexperienced pigeons, however, did not show this reaction when they were clock-shifted. A series of experiments involving test birds of various ages and flying experience suggested that the sun compass as an orientation mechanism becomes available only after the birds had gathered a certain amount of flying experience (Wiltschko, Wiltschko, 1981). Untrained pigeons younger than ca. 3 month did not seem to be able to use the sun compass yet. - This finding appears to be inconsistent with earlier observations that inexperienced pigeons need the magnetic field and the sun to be oriented (Keeton, 1974). The apparent contradiction may be explained by assuming that young birds, before the sun compass is developed, use the sun as an infinitely far, parallax-free "landmark" to maintain straight flying direction (comp. Wiltschko, 1983). This hypothesis is supported by the finding that inexperienced pigeons that were raised without ever seeing the sun, and thus probably learned to maintain straight courses by other means, were normally oriented under overcast (Wiltschko et al., in prep).

Experiments studying the development of the sun compass showed that the directional relationship between sun azimuth, time and geographic direction must be learned. When young pigeons were raised in a permanent 6 h slow clockshift (i.e. their day always started 6 h after sunrise and ended 6 h after sun set) they developed an abnormal sun compass which was adapted to

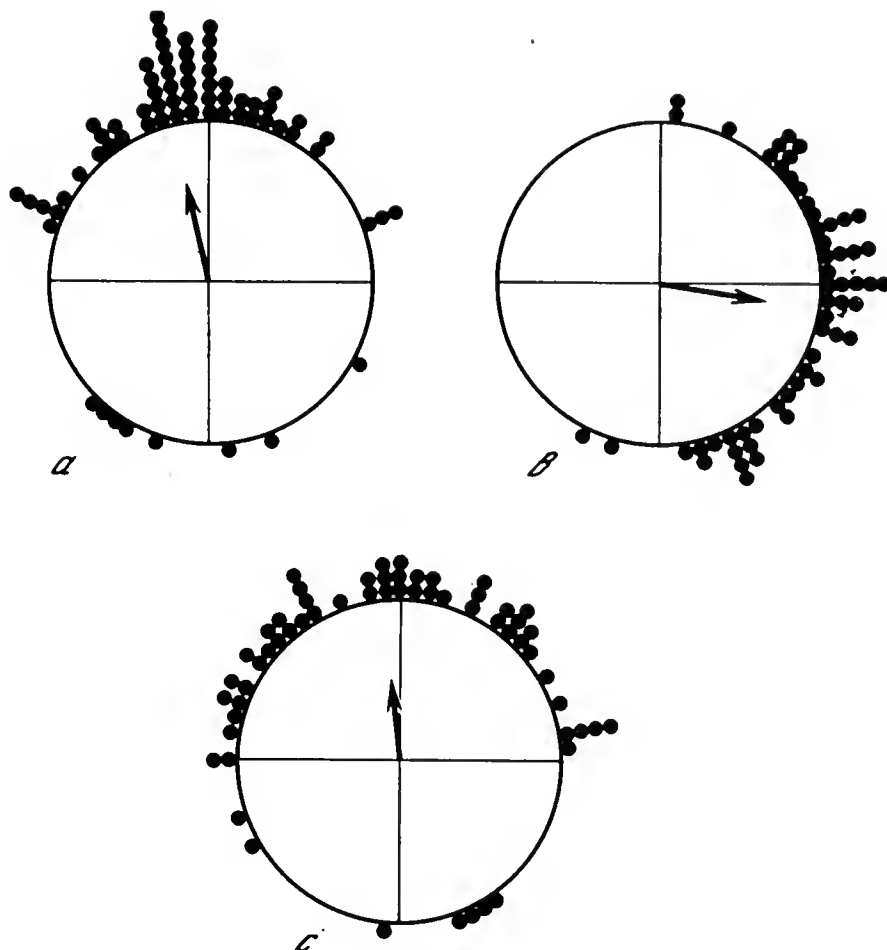


Fig. 3. The sun compass of homing pigeons is established by experience
a - untreated controls were homeward oriented (home $\hat{=}$ upward). b - pigeons whose internal clock had been shifted 6 h slow exhibit the typical clockwise deviation indicating the use of a time-compensating sun compass. c - pigeons raised without ever seeing the sun in the morning were homeward oriented when they were released in their subjective morning with their internal clocks shifted 6 h slow. This indicates that they could not use the sun compass during a time of day when they had not seen the sun before.

The symbols at the periphery of the circle mark the vanishing bearings of individual pigeons; the mean vector is represented by an arrow with the length drawn proportional to the radius of the circle. Data from R.Wiltschko, W.Wiltschko (1980)

the experimental situation. Shifting then back to natural time had the same effect as clock-shifting has on normal birds (Wiltschko et al., 1976). A further analysis of the learning process revealed that the birds must observe the sun's arc at various times of the day to establish a sun compass for the entire day. Pigeons that knew the sun only in the afternoon after culmination did not use the sun compass in the morning (Fig. 3); they used the magnetic compass instead (Wiltschko, Wiltschko, 1980; Wiltschko et al., 1981). In the next series of experiments we tried to answer the question what reference system underlay the sun compass, i.e. how the birds calibrated the sun's movements. The magnetic compass was an obvious guess, and we indeed got evidence indicating that the magnetic compass is involved. Our findings, however, seem to suggest that the relationship between magnetic compass and the sun compass might be more complex than a simple calibration (Wiltschko et al., in prep.). Establishing the sun compass by observing the sun's arc offers the great advantage that the pigeons' sun compass is always adapted to

the local situation and can compensate correctly for the varying rates of change in azimuth at that specific geographic latitude. It is also possible that the learning process continues after the mechanism has begun to function, adapting the sun compass to the seasonal changes in the sun's arc. Later experiments with former permanently clock-shifted pigeons, at any rate, seemed to indicate that their abnormal sun compass could be re-adapted to the natural situation (Wiltschko et al., 1976).

As soon as the sun compass is established, it becomes the preferred compass mechanism of pigeons. It is used at distant locations as well as in the immediate vicinity of the loft (Graue, 1963). Its information supercedes magnetic information as long as the sun is visible. The magnetic compass has then lost its originally important role and serves mainly as a back-up system on overcast days.

CONCLUSION

Thus in the orientation of night migrating birds, as well as in the compass orientation of homing pigeons, we find that simple compass mechanisms serve as a basis for the establishment of highly complex, learned mechanisms which are later preferentially used. The same appears to be true in the third orientation context not discussed in this paper, namely the establishment of the "navigational map" used to determine the home direction after displacement (comp. Wiltschko, Wiltschko, 1982). Such a procedure allows the birds to make use of a multitude of environmental cues of diverse nature, and thus ensures that the various sources of information can be effectively utilized.

ACKNOWLEDGEMENT

We thank V. Bingman for critically reading an early draft of this manuscript.

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THE ROLE OF MAGNETIC INFORMATION IN BIRD ORIENTATION

P.Semm and W.Wiltschko

Department of Zoology, J.W.Goethe-University, Frankfurt a.M.,FRG

INTRODUCTION

In the past 15 years growing evidence has accumulated that the geomagnetic field can influence the behaviour and orientation of a variety of organisms from bacteria through vertebrates (for review, see Wiltschko, 1980). From this body of experimental work it seems important to note that most behavioural responses generally fall into two categories: either they involve magnetic compass orientation, or, in addition, imply some form of physiological sensitivity to weak fluctuations in natural magnetic intensity, i.e. the extraction of time or map information from changing background geomagnetic activity.

THE MAGNETIC COMPASS

Before the magnetic compass was found in birds (Merkel, Wiltschko, 1965), the sun compass and the star compass had already been described, and thus the magnetic compass was at first considered a second order mechanism, used only, when the use of the sun or the stars was prevented by adverse weather conditions. However, additional findings soon indicated that the magnetic compass played a much more important role in bird orientation, and suggested that it might represent the fundamental component of the bird's directional reference system (Wiltschko, Wiltschko, 1976), by which the other factors used for directional orientation can be calibrated.

The magnetic compass is much simpler than any mechanism involving celestial information as the sun and the stars change their positions with time and with geographic latitude. These temporal and spatial variations must be taken into account, since seeing them alone does not provide the basis of a direction finding mechanism. Whereas the astronomical systems are established by learning processes, the ability to perceive the magnetic field provides the bird with a reference system at birth. To check whether or not the natural magnetic field might play a role in the learning processes which led to the establishment of celestial compasses, two species of migratory birds were tested in an experimental situation where the magnetic field and the stars provided conflicting directional information (Wiltschko, Wiltschko, 1972). In this experimental situation the birds changed their directional tendencies and adjusted their direction of migratory restlessness to the magnetic direction only.

This finding and the results of other experiments suggested that the magnetic compass is the bird's primary compass mechanism, implying that information from the magnetic field is transferred to the stars. This concept holds also true for the use of the sun compass in pigeons: pigeons that had never seen the sun before noon could not use the sun compass in the morning; nevertheless they were homeward oriented. When such birds carried magnets, they were disoriented, suggesting that they were using the magnetic compass. These findings indicated, that the magnetic compass is available to pigeons whether or not the sun compass had established and that the magnetic compass

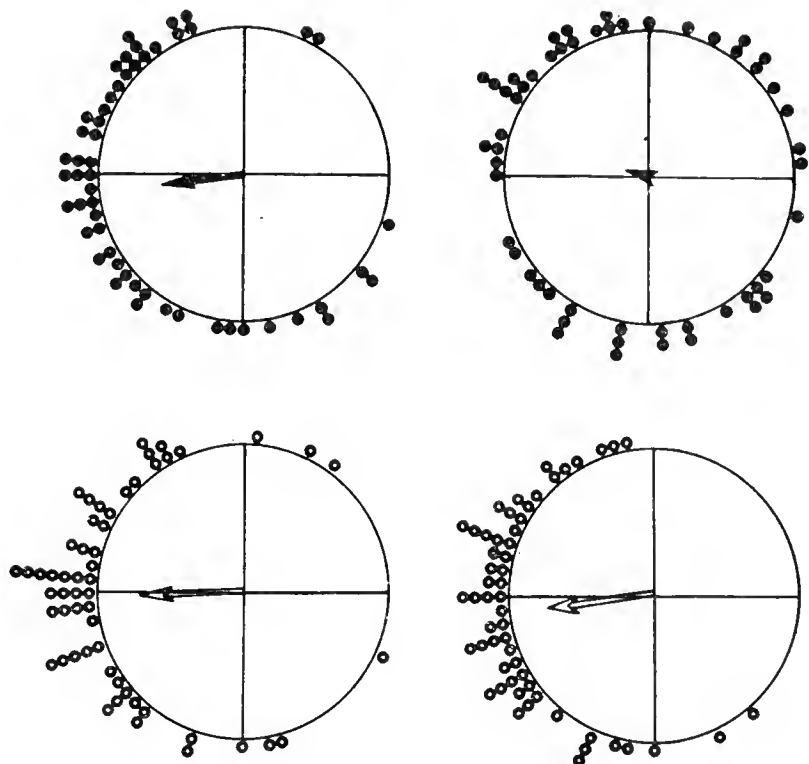


Fig. 1. When released early in the morning, the control pigeons (A) were oriented, and so were the experimentals that had never seen outside their loft at that time of day (B). Magnets did not affect the orientation of the controls (C), but the experimentals with magnets were no longer oriented (D). The vanishing bearings of individual birds are represented by the dots outside the circles, and the mean vectors are shown as arrows whose lengths are drawn proportional to the circle of radius 1 (from R.Wiltschko et al., 1981)

is apparently the first source of compass information, preceding the use of the sun, which is the preferred compass of experienced birds (Wiltschko, Nohr, Wiltschko, 1981; see also Fig.1).

To act as a basic directional reference system for birds is not the only function of the magnetic compass. Several findings suggest (for review see Gould, 1982), that magnetic directional information gathered 'en route' is used to determine where home lies, implying that magnetic information is not used only during active flying but also during passive displacement.

Young pigeons are apparently able to register that they are transported for example magnetically southwards and they reversed this direction and flew northwards to come home (Wiltschko, Wiltschko, Keeton, 1978), whereas older and more experienced birds normally employ different strategies. Recently Wiltschko and Wiltschko (1981) could demonstrate that light is an important prerequisite for sampling magnetic information during an outward journey of young unexperienced pigeons (see also Fig.2), supporting thus the hypothesis of Leask (1978) that magnetic field detection could take place in the retina, mediated by rhodopsin.

By contrast, in elder animals any effect of treatment during transportation is minimal, and we must assume that they switch to using sitespecific information as soon as they become familiar with it (Keeton, 1974). The ideas about the nature of such map factors are unfortunately still very vague, but some observations suggest that the magnetic field is somehow involved (Keeton et al., 1974).

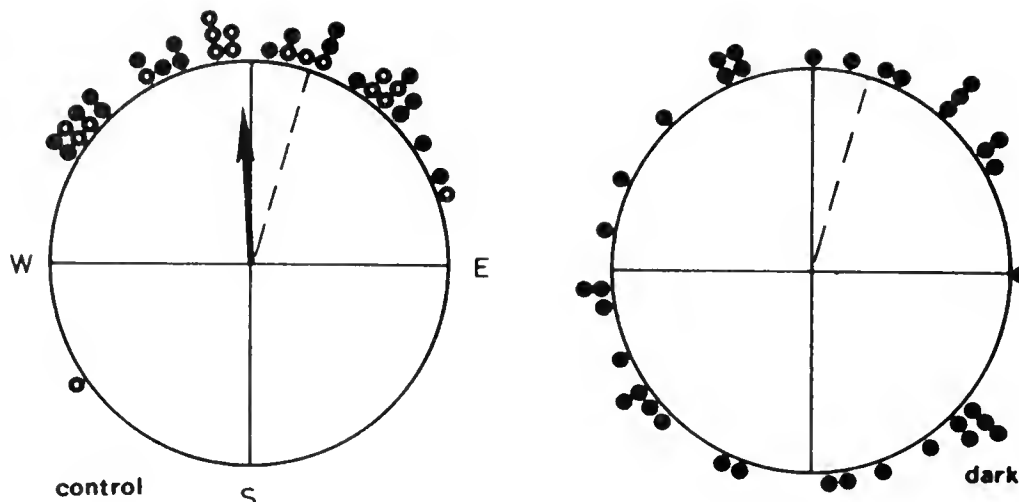


Fig. 2. Summary of the four tests demonstrating the effect of total darkness during the outward journey. a - both types of controls were significantly oriented ($n=37$, $R=357^\circ$, $r=0.076$, $P<0.001$); b - the birds transported in total darkness showed random behaviour ($n=37$, $R=137^\circ$, $r=0.01$, $P<0.05$). The departure bearings are represented by the symbols at the periphery of the circles; the mean vectors are given as arrows with the length r drawn proportional to the radius of circle=1. The home direction, 17° NNE, is marked by a dashed line (from W. Wiltschko, R. Wiltschko, 1981)

SENSITIVITY TO SMALL MAGNETIC FLUCTUATIONS

There is another effect of the earth's magnetic field on the orientation of birds, which is entirely different from its use as a compass. The work of Wiltschko and Merkel (1971) and of Wiltschko (1972, 1974) has indicated that the compass of migratory birds is protected against changes in the magnetic environment. When robins were adjusted to field intensities outside their normal functional range, they could use these fields for orientation, while maintaining the ability to read the natural geomagnetic field they had been accustomed earlier. Birds apparently have the ability to adjust to any given intensity separately.

Southern (1971), working with Ringbilled Gulls, has obtained data that suggest a sensitivity to magnetic fluctuations of less than 50 gamma (the natural magnetic field is in the range from 0.4-0.6 Gauss = 10^5 gamma = 10^{-4} Tesla). Because of the daily heating and cooling of the atmosphere displaces the jet stream north and south, a more or less regular circadian variation of the intensity of the magnetic field is observed on the ground and after solar flares an enormous number of extra ions appear in the jet streams, causing irregular changes in the magnetic field (less than 100 gamma). These storms have roughly dosage-dependent effects on birds (Keeton et al., 1974), indicating that the magnetic sensitivity of pigeons is in the range of 10-30 nTesla. Since even a 1.000 nTesla storm could not rotate a compass needle even 2° , and since these effects on pigeons and gulls are observed when the sun is clearly visible, the phenomenon is discussed as being possibly related to the map sense (Gould, 1982). On the other hand, these findings make it probable that the nearly circadian rhythmicity in the magnetic field intensity could be used as a time cue, an idea, which is discussed later in relation to the findings of magnetic sensitivity in the pineal gland (Semm, 1982).

From this point of view it is a problem that strong magnetic fields and Helmholtz-coils normally do not destroy orientation on sunny days (Keeton,

1971), posing the question how pigeons could possibly measure such minute field changes in the presence of strong static fields. As shown by Larkin and Keeton (1976), however, the vanishing bearings of pigeons given such strong field treatments correspond to those seen on days with magnetic storms, suggesting a map effect. Moreover, when magnetic equipped pigeons were released at magnetic anomalies (Walcott, 1982), the effects of these geographical disturbances persisted.

In conclusion, it might be suggested that a magnetic map detector must attend only to the small changes between and around both loft and release side, and ignore the larger background fields, which are essential for the cloudy day compass system. Such a map must have a long time constant as pigeons can fly through anomalies with little effect and the animals do not recover from releases at anomalies until they have been out of the field for some time.

A MAGNETIC SENSORY SYSTEM IN THE BRAIN?

A final problem for the magnetic compass and a magnetic map system is how the nervous system could measure direction and small intensity changes. Whether or not the recently discovered single domains of magnetite in pigeons (for review see Kirschvink, 1981) have anything to do with pigeon magnetic orientation is unclear until yet. In the opinion of the authors, the involvement of magnetite crystals requires a sense organ, which must be equipped with sensory hairs to be enabled to monitor movements of magnetite within the magnetic field. To our knowledge, however, such an organ has not been described.

On the other hand, magnetic sensitivity could be demonstrated in the central nervous system of rodents (Semm et al., 1980; Welker et al., 1982) and pigeons (Semm et al., 1982; Mai, Semm, 1982), without any evidence for a specialized sensory organ. However, it cannot be excluded that a possible input from a specialized magnetic receptor is incorporated in the data described below. In the pigeon, single unit recordings in the pineal gland reveal that about 30% of the pineal cells recorded respond to changes in both the direction and intensity of the natural magnetic field, some cells exhibiting a magnetic sensitivity of 0.0001 Gauss (Semm et al., 1982; see also Fig. 3c).

Since this structure is a light-sensitive time-keeping organ (for review see Vollrath, 1981), it was discussed as forming one part of a combined magnetic-compass-solar-clock system, which might be involved in sensing and/or transmitting possibly time dependent magnetic information from the environment.

Moreover, the melatonin synthesizing enzyme N-acetyl-transferase in the pineal gland of rats (Welker et al., 1982) and in both the retina and pineal gland of quails (Cremer-Bartels et al., 1982) could be shown as being sensitive to changes in the magnetic field. An important result of the investigations in the rat pineal was that the melatonin synthesis was depressed differently by the magnetic stimulus at different time points during the night. Whilst an inversion of the horizontal component of the magnetic field at 22.00 hours caused a depression for some hours, the same stimulus given at midnight inhibited the hormone synthesis for one hour only. This indicates, that an internal rhythm of magnetosensitivity may be present in the pineal and further behavioral investigations with pinealectomized pigeon have to show whether or not the pineal is part of the earlier discussed magnetic map

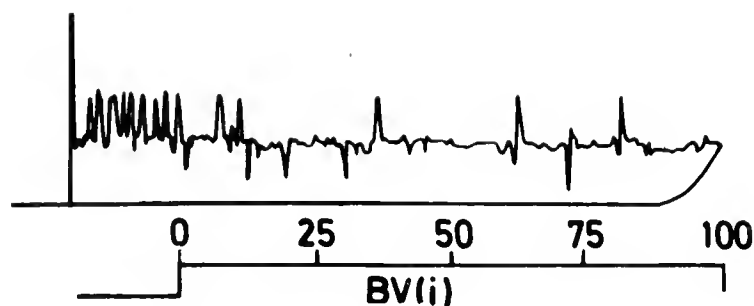


Fig. 3. Electrical activity of a pigeon pineal cells which was summed by an averager system with a time base of 500 msec per bin (total bin number = 256; a bin is the period of time during which the incoming electrical potentials are summed). The picture shows a peri-stimulus time histogram of a pineal cell, which showed at the beginning of a gradual change in the vertical component of the magnetic field ($B_{V(i)}$) a marked rapid depression of activity (0 on the underlying scale is the natural magnetic field, 100 is the complete inversion). Further gradual changes towards the complete inversion caused no additional changes in activity. It should be noted that the initial reaction was apparently due to a minimal change (0.001 Gauss) in the magnetic sensitivity at least in this cell was very high (from P.Semm et al., 1982)

rather than being involved in compass orientation. Recently, Maffei and co-workers (pers. communication) have demonstrated that pinealectomized pigeons were capable of homeward orientation in overcast conditions, though the bearings of experimental animals were rather more scattered than those of the controls. The recorded effect was similar, but somewhat smaller than that produced by magnets applied to pigeons released under overcast skies (Keeton, 1972).

In another study, using the (^{14}C)2-deoxyglucose technique (Sokoloff et al., 1977), the functional uptake of the substance induced by earth strength magnetic stimulation revealed different brain areas in the pigeon probably involved in detecting and/or transmitting natural magnetic fields. Those regions exhibiting extensive glucose uptake as compared with controls included the molecular layer of the cerebellum, the optic tectum, the parvocellular component of the isthmic nuclei, the intercollicular nuclei, the vestibular nuclei, the trapezoid body and the epithalamus, including the habenular nuclei and the pineal gland (Mai, Semm, 1982). The occurrence of an intense labeling of the pineal gland, even during daytime, when the secretory activity is low and during the night following stimulation with light, presents additional evidence for a specific magnetic sensitivity of this structure. In view of the fact, that the melatonin synthesis is inhibited by magnetic fields, it appears meaningful, that some brain areas which contain melatonin (cerebellum, visual system, brain stem) are also responding to magnetic stimuli.

It may be worthwhile to note that the magnetic stimuli used in this study (inversion of the horizontal component) cover only a small range of possible direction- and intensity changes which might occur in the natural environment. Thus, using another stimulus, the metabolic mapping may be different in some parts of the brain. Further experimental studies are required in order to clarify the relative importance of the demonstrated magnetic areas in pigeon magnetic orientation.

CONCLUSIONS

The great importance of the magnetic compass as a reference system for both the star- and the sun compass is described. The possibility of using directional information collected relative to a compass system during an outward journey is discussed.

The sensitivity of birds to small magnetic fluctuations is discussed with its possible relationship to the internal map, which is important for determining the home direction in experienced pigeons. The possibility of a magnetite based sensory system and the results of magnetic sensitivity in the pineal gland and other parts of the central nervous system are critically described.

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STUDIES ON BIRD ORIENTATION IN THE USSR

V.D. Ilyichev

Institute of Evolutionary Morphology and Ecology of Animals of the USSR
Academy of Sciences, Moscow, USSR

I am greatly honoured that I can tell you about the work of my compatriots working in various laboratories in the USSR. Unfortunately, the time assigned to me is limited and I can not describe the work of each colleague so comprehensively as it deserves to be described. However, the monograph "Space orientation of birds" (1978) that we have jointly prepared with E.K. Vilks contains a detailed compendium of all the published works and comprehensive data on all the works carried out at present. Therefore, I need not to retell you its contents.

At the same time, I would like to use the time assigned to me for analyzing the approaches and logic of our studies since the program outlined has not been completed yet, it is now being carried out and we expect certain results from it. This program is not traditional, at least in some of its parts and in our opinion it is worthy of consideration.

Of special importance for my colleagues was the fact that in the mid -70s we embarked on tackling the problem of orientation, lacking unlike our colleagues in other countries sufficient experience in this kind of research which had its positive and negative aspects.

Of much importance for us was the partnership with entomologists, ichthyologists and theriologists who at that period started to develop a complex program "Space orientation of animals and means to control their behavior". This program covered all the analyzer systems, their role in the orientation and communication of all groups of the animal world.

The investigations bore a complex character, they used ecologo-morphological and ecologo-physiological approaches and methods and as a result ornithologists found themselves with their object of study in the area of research which was not quite traditional for them.

Orientation of birds as a field of research, due to its venerable age and established traditions, has always stood apart and used its own methods and hypotheses reflecting the biological specificity of birds.

Ornithologists emphasized the fact that orientation of birds is something special in the animal kingdom, therefore it required its own methods of investigation. Surely, these approaches have been correct in many respects and played a positive role, but some other factors should also be taken in consideration.

The birds had their evolutionary precursors, therefore much of what they had possessed was inherited by the birds. This required naturally a certain isolation in the studies of birds orientation, on one hand, and on the other hand contacts with colleagues studying these phenomena in the other groups of the animal kingdom.

Thus, the ecological aspects of birds orientation have been outside the scope of ornithologists' concern for a long time. In the meantime, orientation as a phenomenon is highly ecological since it provides the existence of birds in space, which should be continuously perceived, controlled and evaluated from the ecological point of view. And of course, it is necessary to predict

the development of events with respect to their ecological significance. Therefore, we can understand orientation as an adaptive phenomenon, provided its ecological trend is taken into account both as a whole and in detail.

Extensive analytical work for evaluating the available material has been carried out by the ornithologists headed by H.A.Mikhelson at the Biological Institute, Acad. Sci. Latvian SSR (Riga).

As has been expected, a considerable part of the available material proved to be inadequate and had to be removed from circulation. Special attention was given to the correct formulation of the experimental task and to the criteria of this formulation. Statistical methods of data processing were particularly emphasized.

Having analyzed the suggested hypotheses from this point of view, H.A.Mikhelson singled out the most probable and convenient ones for experimental testing.

The first investigations dealt with non-visual orientation of birds. Tests were carried out at a high technical level. Extensive material was obtained.

The traditional methods were noted for serious shortcomings. Non-visual orientation of birds in closed spaces under given test conditions manifested itself to an insignificant degree. Therefore, special attention was given to the improvement of the methods and to critical comprehension of the literature on bird orientation. The precision was enhanced and data recording during tests was automated, a new mathematical basis for digital data processing was introduced. Various models of visual astronomical reference points came into use, a special planetarium was built making it possible to displace the direction of the stellar and magnetic meridian at different angles between each other and with respect to the geographical meridian. Various devices aimed at studying the orientation behavior of birds under controlled environmental conditions were employed.

As a result of numerous experiments, it was found that the orientation of the birds studied (Erithacus) during migratory restlessness is determined mainly by available visual sources of spatial information. The dependence on the direction of the magnetic field meridian did not manifest itself. Upon presentation of the planetary stellar sky to the birds the direction of their movements depended on the luminosity vector. There are reasons to believe that the open reaction of photovectorial orientation is a component part of the physiological mechanism maintaining the migratory direction in birds. Presentation of a single fixed light reference point induced compensatory responses ensuring selection and maintenance of migratory direction by separate natural moving astronomical reference points. Based on these tests two original hypotheses for astronomical orientation of night migrants were put forward: orientation of birds by separate stars or star clusters (V.K.Liepa) and the decisive role of the sun in selection and maintenance of the migratory direction by night migrants (E.B.Katz). These studies resulted in the discovery of orientation responses of photocompass and photovestorial type, the components of the orientation biological mechanism.

Among the few hypotheses in the field of orientation, Middendorff's hypothesis proposed in 1855 was one of the first. In the last few years the magnetic hypothesis has drawn scientists' attention again.

In the middle 70s V.R.Dolnik and M.E.Shumakov, orienthologists of the Zoological Institute (Rybachiy), carried out a series of experiments in the region of Kursk Magnetic Anomaly. Using the round cage method they showed that the birds captured in Rybachiy were capable of orienting under conditions of anomalous geomagnetic field remote from their habitat. Later on, Latvian ornithologists and those from Kiev University were testing the magnetic hypothesis. This work is still going on. For ornithologists of Zoological Institute (Rybachiy) this work initiated a cycle of experimental investigations carried out simultaneously with the program of banding and ecologophysiological studies of migrations.

An interesting experiment was made on Carpodacus and Silvia nisoria brought from the Kurshsk Spit to Dushanbe and, Khabarovsk. While investigating their orientation behavior in round cages, the ornithologists showed that during the fall migration on the Kurshsk Spit it is standard, that is oriented southeast, whereas in Dushanbe the same birds orient to the east and in Khabarovsk to the northeast.

Of much interest are the data obtained in Rybachiy on the accuracy of orientation of Muscicapa hypoleuca displaced far (up to 200 km) from the nest (1-2° in latitude, 2-3° in longitude). Based on these experiments V.R.Dolnik formulated a number of important theoretical concepts, specifically the hypothesis of navigation from the goal.

Ornithologists of Kiev University employed methods of displacement from the nest with subsequent release and recording of the time of return as well as a planetarium with switching off a stellar sky and switching on an artificial magnetic field, rotation of birds, various methods of processing the resulting data. The experiments used Riparia riparia, Delichon urbica, Hirundo rustica, Sturnus vulgaris, Sterna albifrons, S.sandvicensis, S.hirundo, Parus major, Passer domesticus, P.montanus. A study on the nearest homing made it possible to collect extensive material and reach the following conclusions.

Birds have not one but several duplicating systems for orientation and navigation, which are triggered in parallelly or in succession, providing high reliability and accuracy of navigational determinations. Landscape reference points are hardly used by migratory birds in homing, however in non-migratory birds this is the chief and possibly the only system of orientation.

The navigation abilities, manifested in homing, develop in birds as a result of training. Untrained starlings grown in open-air cages of Askaniya Nova could not find their way "home" which confirms the hypothesis about the role of post-nesting migrations in the development of navigation abilities.

Starting directions coincide with the direction of spring and sometimes fall migration. Birds displaced 20 km from their "home" show rapid and accurate determination of their position. Various species show a maximum speed when displaced 30 km from their nests. When taken 60 km away, their speed decreases apparently due to time spent on feeding and rest.

Solar navigation of birds is effected by using such parameters as the height and positional angle of their movement.

Lack of visual astronomical reference points does not affect the reliability and speed of navigational determination of the course. They select the

starting direction in the same way as in the case of the Sun and the speed of returning "home" does not decrease.

The use of magnetic orientation is confirmed by experiments in a planetarium and open air with the application of artificial magnetic fields. A correlation was noted between the coefficient of bird orientation and the index of geomagnetic field disturbance. The orientation coefficient rises with the increase of the Earth's magnetic field.

Generalizing articles and monographs were of special importance in the work of our ornithologists on this problem.

Kumari (1975) and Dolnik (1975) dedicated separate chapters to this problem in their monographs, as well as special generalizing articles on this subject (Kumari, 1965, 1965a). Dolnik (1973) considered an important theoretical problem concerning the types of orientation and their interrelations. Yakobi (1966), Kistyakovski and Smogorzhevski (1970), Vilks (1968) summarized the investigations under way and outlined further prospects.

Special attention was given to signalling aspects of orientation. Considering the partner population as a spatial reference point, K.N. Blagosklonov investigated signal-spatial relations of fledgelings and their parents, fledgelings between each other at different stages of ontogenesis. In these experiments carried out on Muscicapa hypoleuca and other hollow nesting birds K.N. Blagosklonov showed a great role of training and imitation in the development and perfection of orientation abilities. Developing similar ideas W.E. Jacoby put forward interesting considerations about the role of post-nesting block migrations in the perfection of orientation abilities in young birds contacting and imitating each other in their response to surrounding reference points.

The second direction was concerned with studies on the orientation of adult birds at different periods of the seasonal cycle and specifically at their nesting period. Experiments of E.N. Derim-Oglu, K.N. Blagosklonov, early works of E.K. Vilks and other Latvian ornithologists dealt with the role of the nest, its contents and environment as stimuli of orientation behavior and at the same time important signal-spatial reference points. These studies were pursued to some extent by A.I. Promptov, whose works dealt with nest instincts and carried out in the 30-40s.

Of special interest from the viewpoint of orientation were the experiments on displacements of nests within and beyond the nesting areas, deformation of nests, replacement of eggs and fledgelings, changing of their number, etc.

The third direction revealed and studied the ecological correlates of analyzer systems providing perception of population and biocenotic partners acting as reference points.

Using the acoustic orientation of owls in response to reference points biologically important for them (voice of fledgelings, squeaking and rustling of mice) as a main object, T.B. Golubeva, L.I. Barsova, V.D. Anisimov, A.T. Chornyi, V.S. Voronetski together with the speaker identified and studied their adaptations providing orientation of the birds as an ecological phenomenon.

Studies on the ecological aspects led to an important scientific generalization: analogization of orientation behavior with induced behavior of birds. The need to control the behavior of birds by repellents and appetents has become

one of the most important practical problems. Protection of cereals and fruit cultures from birds, prevention of collisions between airplanes and birds, control of pests by using birds required some means for attracting or repelling birds. This field developed empirically and its further advances depended entirely upon new theoretical approaches.

First of all there was a need for an ecological analogue of controlling the behavior of birds, the study of which under natural conditions would make it possible to implement the model perfected by the nature into the practice of repelling and attracting the birds. Having proposed the behavioral response of a group to the presentation of reference points as such an analogue, we discovered a number of group orientation phenomena which later on formed the basis for new methods of controlling the behavior of birds.

While considering the control of behavior as a modelling of orientation behavior, we were able to use in practice the specific features of bird orientation, which had been perfected by the natural selection for a long time. The practice of controlling behavior has become a kind of consumer of data provided by ornithologists investigating the ecological aspects of bird orientation.

These are the tendencies and the logic of advances in the studies, as I see them. Naturally, my analysis is subjective and I bring my apologies in advance. I would like, however, to emphasize the fact that the ecological correction alongside with the traditional, analytical approach in the studies of orientation is entirely justified. It seems to me that the way of interaction of these two trends is a promising one and can give interesting results in the future. However, in order to make this a reality, it is necessary to extend the concept of orientation itself in structural and functional respect.

In its general form, orientation should be regarded and studied as a complex system composed of many interacting analyzers, subject to many biotic and abiotic factors, solving and serving many ecological problems (including migratory ones) based on perception of numerous reference points and environmental phenomena.

Assuming the most general definition, we should study the manifestations of orientation abilities, which serve particular ecological problems, including migrations. In this case, each problem will form around itself a special trend in orientation studies, which is more or less independent with respect to goals, methods and traditions. All these trends complement each other and will create a concept of orientation as a broad adaptive phenomenon playing an important part in life of birds.

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Symposium

STRATEGIES OF BIRD CONSERVATION

Convener: S. TEMPLE, USA

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LOVEJOY TH.E.

MINIMUM SIZE FOR BIRD SPECIES AND AVIAN HABITATS

BURNHAM W., CADE T.J.

REINTRODUCTION AND TRANSLOCATION OF BIRDS AS CONSERVATION
STRATEGIES

TEMPLE S.A.

MANAGING BIRD POPULATIONS VERSUS MANAGING THEIR ECOSYSTEMS

IMBODEN C.

PRIORITIES FOR EXTINCTION

MINIMUM SIZE FOR BIRDS SPECIES AND AVIAN HABITATS

Thomas E. Lovejoy

World Wildlife Fund US, Washington D.C. 20009, USA

Continuing constriction of wild areas by economic development lends added urgency to the charge of conservation. With greater pressure on the land the question of the size of conservation areas becomes yet more important, there being little point in protecting areas too small to fulfill their purpose on a long term basis. The problem of size is on the one hand, largely irrelevant for those species such as the American robin (Turdus migratorius) favored by domestic landscapes and, on the other, is highly complicated for migratory species with series of areas and requirements along their annual routes.

Even when considering a conservation area for a single species of relatively sedentary nature, size of the protected area can be a difficult question if the autecology is poorly known. For such species, incidence functions, which plot the frequency with which a particular species is found on islands of different size classes, can be very useful (Diamond, 1978). Some species are found on all islands of all sizes, but others have an s-shaped curve, indicating there is essentially a threshold island size below which the particular bird species does not occur. Terrestrial islands set in human altered landscapes can also provide data of use from this point of view. In the case of both real and habitat islands, it is important that the vegetation among the islands be essentially consistent if the incidence function is to be reliable from the point of view of long term conservation. Not only is it likely that a number of species will not occur in a sufficient number of habitat patches or islands for such functions to be constructed. It is also possible that the habitat fragments or islands will not be in something approximating an equilibrium state (albeit a dynamic one subject to species turnover) and therefore no more useful for incidence functions than had they very different vegetation.

The tendency of newly isolated fragments of habitat or land bridge islands recently cut off from a main land to lose species after isolation is now widely recognized (Diamond, May, Terborgh, Lovejoy, Oren, 1981) and presents a very serious problem for conservation (Lovejoy, 1980). Deduced from the species of birds found on islands of varying size (Diamond, May, Terborgh) it has been similarly deduced from bird species found in woodland fragments of varying size (Forman et al., Galli et al., Moore, Hayrer, Whitcomb et al., 1982; Willis, 1980). In a growing number of examples, so far from only North and South America, actual species loss from isolated woodlots (Leck, Whitcomb et al., 1982; Lovejoy et al., in press) as well as from a newly created island, namely Zarro Colorado in the Panama Canal, has been documented.

Aside from the recently initiated minimum critical size of ecosystems study in the Central Amazon (Lovejoy, 1980; Lovejoy et al., in press), the best documented example to date is that of Zarro Colorado. Willis (1974), analysing data from the time of isolation in 1914-1917, compiled the list of bird species lost and attempted to distinguish between those lost from the vegetational succession and those lost because of the presumed area effect. Morton (1978) subsequently reintroduced two species of wren which had disappeared; neither reintroduction was successful, and while they shed light on the

possible imminent causes of their loss, it can still be argued that their original disappearance could be attributed to the area effect. Reintroduction nonetheless can be a most useful tool in understanding at least the imminent causes of species loss and thus how a reserve might be managed to favor rather than disfavor persistence of such species.

Terborgh and Winter (1980), in an analysis of island data, suggested that the species loss process was largely important as far as size, trophic level and taxonomy was concerned, and suggested that rarity was the best indicator of the vulnerability of species to being shed by an isolated habitat fragment. This would automatically include large top predators, other large species, habitat specialists (providing their particular habitat was not very abundant) and species near the limit of their ranges. Species such as frugivores and nectarivores which must move about considerably in search of resources would be rare in this sense and vulnerable as well.

Karr (1982) recently reexamined the Zarro Colorado data. He questioned whether the high populations of small predators, especially coatimundi (Nasua narica) which had been implicated in the loss of a number of bird species could properly be attributed to area effect. Karr pointed out that large predators, the absence of which from Zarro Colorado had been linked by previous authors to the high populations of smaller predators, were also absent from the main land area where small predator populations were low. Yet hunting pressure on the main land which Karr indicated was responsible for low populations of large predators would also be equally likely to depress the numbers of small predators. So the point is not conclusive and the islands high numbers of small predators could well derive from the area effect.

Karr also noted that the lack of major streams on Zarro Colorado, a factor responsible for the failure of one of Mortons reintroduced wren species, had historically prior to isolation made the area only wet season habitat for many foothill species. Subsequent to isolation, such species had no recourse to wetter habitat during the dry season and hence encountered difficulties in persisting.

This in part explains the bias toward loss of forest interior species, regardless of abundance, as contrasted those of higher reaches of the forest. In a note added in proof, Karr also raises the important point that in many instances canopy species are superior dispersers and such birds are able to depend on adjacent forest areas and not exclusively depend on resources of Zarro Colorado. Indeed, minimum area for bird species of the canopy such as macaws and toucans can probably be met by a mosaic of forest fragments. Yet even in such cases the fragments must be large enough or close enough for pollinators of key food trees to initiate fruit production and ultimately reproduction of the tree species.

The Minimum Critical Size of Ecosystems project near Manaus, a joint project of Brasil's National Institute for Amazon Research (Instituto Nacional de Pesquisas de Amazonia - INPA) and World Wildlife Fund is taking advantage of land clearing practices to study the ecology of forest patches of varying size both before and after isolation. The smaller patches which will yield simple results rather quickly, also can include a number of replicates so that predictability of the sequence of species loss and terminal species assemblages

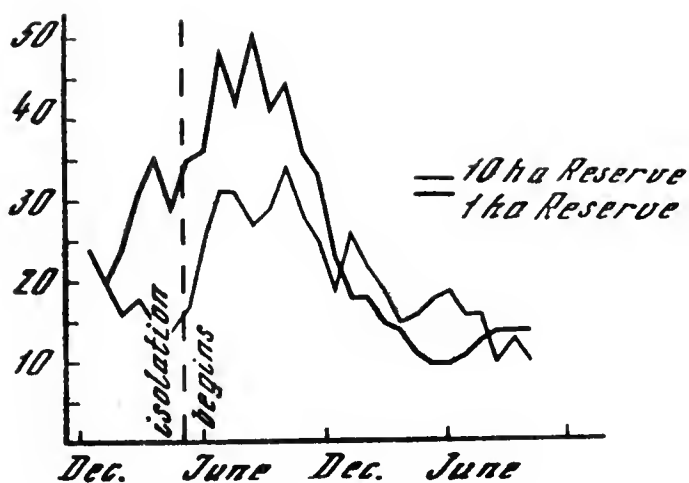


Fig. 1. Seasonal changes of bird activity in two reserves of different size (1 ha and 10 ha)

can be measured. It is likely that the founder effect from the sampling effect involved in saving a small fragment of a large diverse ecosystem (Karr, 1982; Lovejoy, 1981; Lovejoy et al., 1982) will be a larger factor the smaller the patch. In smaller patches the more abundant species will remain likely to be included in the founding population, but while some rare species will certainly be among the founders, the particular ones will be less predictable. Karr (1982) did not detect this among the birds loss pattern at Zarro Colorado, but it must have been involved in the San Paulo woodlots reported on by Willis.

It is also likely that the smaller plots will each have two terminal assemblages of bird species: one reached fairly rapidly from the immediate effects of isolation and one reached more slowly as the tree community changes in both species composition and physical structure. This statement is probably an exaggeration of the pattern to be actually observed in nature because the two factors will be operating together at the outset, albeit at very different rates. For a one hectare plot of Central Amazon forest, the initial change occurs in a matter of months.

To date there is not a great deal to report because only two plots, one of ten hectares and one of a single hectare have been isolated. (A number of additional plots will be isolated in 1982 including ones of 100 hectares). Among the bird species lost in the two initial isolates are two obligate army ant followers: Pithys albifrons and Gymnopithys rufigula. There are species requiring large areas (Bierregaard, ms.) because of their daily requirement for swarming army ant (Eciton) colony. These also constitute an example of species disappearances linked to a common ecological system. Edge species have, of course, increased.

An important result is the instantaneous increase of capture rate of birds in the two reserves as soon as the surrounding understory was cleared. This was probably caused both by an influx of birds from surrounding destroyed understory as well as by increased activity on the part of resident birds with home ranges truncated by the vegetation destruction. The doubled capture rate is significant by the T test. What this means is that superimposed on the species loss function induced by reduction in area is an overpopulation problem. This has been but rarely noted (Fogden in Sarawak, Whitcomb et al., Cabin Fohn Frs.?) and must be of greater importance for smaller vs. larger areas (Fig. 1).

Area considerations apply not only to resident birds but apparently also to migratory species. Whitcomb et al. (1981) in a detailed analysis of bird

distributions in the state of Maryland indicate a number of species of migratory forest birds, e.g. black and white, wormeating warblers, are very sensitive to habitat fragmentation. Also they found a strong positive correlation between forest fragment size and the number of forest interior species. Other species, including two of the forest interior (Acacia flycatcher and scarlet tanager, used smaller forest patches; most of these included birds of edge as well as forest interior. Whitcomb et al. attribute the decline in species number in forest fragments to reduced rates of colonization by birds from elsewhere.

There has been considerable discussion in the recent literature about ideal reserve size, and whether a large reserve will hold more or fewer species than a series of smaller reserves of same total area. The evidence in favor of a series of small reserves has been derived from organisms other than birds: mangrove insects (Simberloff and Abele) and grasses of ancient woods (Game). Arguments based on the theory of island biogeography really depend on the what extent the immigrations, extinctions, and species present on an island or in a habitat fragment are a random set or somewhat structure and predictable. More evidence is needed, of the sort the Minimum Critical Size of Ecosystems project is designed to produce. Yet it is clear from incidence functions, from patterns of loss already known (Zarro Colorado, Min. size project, Maryland forest migrants) that some species tend to either be lost first or are known to require larger areas. That would indicate that some birds could be loosely ranked in terms of area required and that implies in turn that some species can only be protected with large parks and reserves. If one of the goals is to protect communities of bird species then clearly some large reserves are in order.

That does not preclude however, the usefulness of small reserves for particular species, e.g. a small pond for grebes. Nor does it indicate the problem of what is a stable minimum population size, both in terms of ecology and genetics has been adequately solved (Soulé; Soule and Firankel), although incidence functions when constructable for a particular species should provide a good indication.

SUMMARY

One of the major ways in which Man is affecting the biology of the planet is by fragmenting previously continuous habitat. Fragments have a different dynamics after isolation which have important implication for many, but not all, species of bird. This is particularly true for birds of interior of tropical forests. Approaches to determining the minimum area below which a fragment is unlikely to support a bird species or community were discussed.

REINTRODUCTION AND TRANSLOCATION OF BIRDS AS CONSERVATION STRATEGIES

William Burnham, Tom J. Cade

Peregrine Fund, Cornell University, USA

Fort Collins, Colorado 80524, Division of Biological Sciences,
Cornell University, Ithaca, New York 14853, USA

INTRODUCTION

Despite the best national and international efforts, human needs for food, fiber, and fuel are resulting in major impacts on the natural environment. Howevermuch conservationists try to preserve wilderness and natural habitats for the future, there is no doubt that the continuing demands of the future, there is no doubt that the continuing demands of the human population will result in severe changes in the earth's environments. Mankind's needs for energy alone will result in major disruptive processes. Increasingly in the future many species will be forced to make adjustments to these changes or face extinction.

Manipulative techniques are just coming to the fore in our practices of conserving and managing threatened and endangered species and other wildlife, but it has now become necessary to consider the possible use of manipulative intervention in any phase of the life cycle of an animal, or plant, if there is a reasonable likelihood that such tampering will promote the survival of the species in question. Such manipulations of endangered species should be aimed at increasing the density and extending the geographic distribution of diminished populations. These goals can be achieved by promoting increased natural reproductivity, promoting increased survival of individuals in an existing wildpopulation, or by establishing new individuals in a population or vacant habitat. Such individuals can be either wild-caught or captive-produced. The Peregrine Falcon (Falco peregrinus) recovery programs in the United States of America provide an opportunity to examine the full spectrum of these conservation strategies for threatened and endangered birds.

Owing mainly to the effects of DDT (DDE) residues on thinning eggshells, the Peregrine Falcon no longer exists as a breeding bird over more than 2.5 million square km of its former range in the eastern United States and Canada, and the species is otherwise reduced in numbers throughout most of its North American range (Fyfe et al., 1976). In many western states where Peregrines once nested in numbers, such as Montana, Idaho, and Wyoming, even now not a single breeding pair is known to exist. Peregrines nesting in Alaska were affected least, but were still reduced to probably less than half of the pre-DDT breeding population (Fyfe et al., 1976).

Four related but administratively distinct recovery strategies have been developed (Table 1), ranging from protection and monitoring (Alaska) to complete restoration, including creation of a new population to occupy vacated habitat (Eastern).

T a b l e 1. Conservation Strategies for Peregrine Falcon Recovery

| Region | Geographic Area | Population Status 1975 | Population Status 1982 | Conservation Techniques Employed |
|------------------|---|---|---|--|
| Eastern Atlantic | Ocean to Mississippi River | Extirpated by ≈ 1960 | Since 1975, 337 peregrines successfully released; Breeding occurring and many returning falcons; DDT levels low; selfsustaining population by 1987 | a. Protection of species and nest sites by law b. Captive breeding (provides 100% of released falcons) c. Reintroduction by hacking (100%) d. Reintroduction into historical habitat (30% of releases) e. Introduction into new habitat (70% of releases) f. Release on artificial structures (70% of releases) g. Monitoring productivity |
| | States of: Montana, Idaho Wyoming, Colorado, New Mexico, Utah | < 15% of sites occupied (n ≈ 170), limited reproduction | Since 1976, 247 peregrines successfully released; some breeding of released birds, many returning; population increasing; high to moderate DDT levels in eggs; recovery by 1992 | a. Protection of species and nest sites by law b. Monitoring productivity c. Captive breeding (provides 80% of released falcons) d. Hatching of wild-laid eggs (provides 20% of released falcons) e. Release by augmentation (25% of releases) f. Release by hacking (70% of releases) g. Release by cross-fostering (5% of releases, terminated) h. Release into historical habitat (90% of releases) i. Introduction into new habitat (10% of releases) j. Release on artificial structures (10% of releases) |
| California | California | < 15% of sites occupied (n ≈ 200) | Since 1977, 79 peregrines successfully released; returning birds; population increasing; low to moderate DDT levels in eggs, depending on area | a. Protection of species and nest sites by law b. Monitoring productivity c. Captive breeding (provides 20% of released falcons) d. Hatching of wild-laid eggs (provides 80% of released falcons) e. Release by augmentation (85% of releases) f. Release by hacking (10% of releases) g. Release by cross-fostering (5% of releases) h. Release into historical habitat (95% of releases) i. Introduction into new habitat (5% of releases) j. Release on artificial structures (5% of releases) |
| | Alaska | > 50% of sites occupied ¹ | Steady increase in occupied sites; population at pre-DDT use levels on some river drainages; DDT levels low | a. Protection of species and nest sites by law b. Monitoring productivity |

¹ The percent does not include coastal populations.

PROTECTION

Scientists, naturalists, and concerned falconers started conservation efforts in the early 1960's. Many states already protected Peregrines from shooting and regulated their taking for any purpose. The first formal federal step was the inclusion of two of the three races of Peregrine Falcon occurring in the U S A on the Secretary of the Interior's List of Endangered Species under the old Endangered Species Conservation Act of 1966 (later replaced by the Endangered Species Act of 1973, Public Law 93-205). In 1972 the Peregrine and other birds of prey came under the authority of the Migratory Bird Treaty Act by modification of the U.S. treaty with Mexico. About the same time use of DDT, the cause of the Peregrine's decline, was restricted in 1972 in the United States, but use of DDT continues in Central and South America where many Peregrines and their prey winter.

The significance of legal protection as a conservation strategy varies according to the organism. Complete protection, which does not even allow for management, is undesirable. For example, Temple (1977) stated that "conservationists literally protected the eastern population of the Peregrine Falcon until it became extinct". Complicated permits and overzealous law enforcement efforts as aspects of this strategy may actually operate negatively in some cases by preventing or altering proper management, by expending limited funds on fruitless procedures, and by affecting public opinion adversely. Public education and enlightened opinion are often more important to protection of a species than laws and regulations.

CAPTIVE BREEDING

The merits of captive breeding of wildlife, especially for purposes of release, have been argued for many years (Conway, 1977). Considering that no source of Peregrines existed in nature from which "excess" nestlings could be captured and translocated for release, no justifiable alternative to captive breeding existed, if restocking or augmentation was to be attempted. In regions with remnant populations, the removal of wild-laid eggs could be justified only when they could be replaced with healthy young from the breeding program.

Large captive breeding programs for Peregrines did not begin until the early 1970's. The breeding of falcons is not like other avicultural efforts and required development of new skills and technology. Further, Peregrines captured after they begin to fly do not readily reproduce in captivity, and since even captive or wild-produced nestlings do not usually breed until two to four years of age, the programs required years to develop. In 1973, for the first time programs of T. Cade (The Peregrine Fund, Cornell University) and J. Enderson combined to breed and rear young successfully in captivity from all three races of North American Peregrines.

The value of captive breeding to each of the four regional Peregrine recovery programs has varied. In the east no alternative existed, and the Cornell University facility (The Peregrine Fund) was established to produce Peregrines to repopulate that region. The Rocky Mountains still contain a rem-

nant population, but the numbers are so few that even if wild pairs could be induced to produce two clutches of eggs rather than one a year, adequate numbers of falcons for recovery would not exist (Burnham et al., 1978). Also, until about 1978 the procedures for captive hatching of thin-shelled, wild-laid eggs had not been perfected. Extensive efforts were made to locate unknown occupied nest sites, but they met with limited success. A second Peregrine Fund breeding facility was therefore established at Fort Collins, Colorado, in late 1974 to provide falcons for release in the Rocky Mountains. J. Enderson's captive population of Rocky Mountain Peregrines, along with western falcons from other private breeders, provided the nucleus for this captive population.

The California population was also dramatically reduced in numbers. Unlike the Rocky Mountain region, extensive nest site surveys provided a number of new pairs in a remote part of northern California. By removing the wild-laid eggs and causing some pairs to lay second clutches, most Peregrines needed for release could be produced by manipulation of wild pairs. B. Walton and co-workers removed wild-laid eggs from the eyries and hatched them at a captive breeding facility established at the University of California, Santa Cruz, California. Walton's program joined with The Peregrine Fund in 1982.

The Alaskan Peregrines were less affected by DDT than falcons in other regions. Some natural production continued to occur, and captive breeding or release of young was judged to be unnecessary there.

The captive breeding programs have been successful. To date over 1,000 Peregrines have been successfully hatched and reared at the Cornell and Fort Collins facilities, which house about 200 falcons. Fertilization of eggs is accomplished either by copulation between paired males and females or by artificial insemination in cases in which mating cannot be achieved. About 80% of all fertile captive-laid eggs hatch, and 90% of the hatched young survive at least until release (Burnham, in prep). In recent years about 90% of all live wild-laid Peregrine eggs brought to the Colorado facility hatched in incubators, and Walton has had similar results in California.

RELEASE AND REINTRODUCTION

Release of captive-bred wildlife is difficult at best and many problems develop (Campbell, 1980). The Peregrine release programs have been no exception; however, over the years procedures have been developed by which large numbers of captive-hatched falcons have been successfully released to the wild in such a way that survivors return when sexually mature and reproduce normally (Cade, 1980, 1982; Barclay and Cade in prep; Burnham et al., 1978). Both nestlings and, in a few cases, adults have been released. With a highly mobile species such as the Peregrine, a period of "site-fixation" must occur before release so that the falcons will return to the release area and breed. The casual release of flying young or adults is not sufficient. The release of young Peregrines without parents, involving an initial period of fixation to locale, is called "hacking" (process explained in detail in Sherrod et al., 1981). Hacking usually involves holding and caring for groups of young falcons at selected sites and allowing them to grow and learn to fly and

hunt while becoming familiar with the area (Cade, Temple, 1977). If breeding adults are present at a site, captive-hatched young of the same age may be added to an existing brood. With Peregrines this process, called augmentation or fostering, usually involves the exchange of captive-hatched young for wild eggs (Burnham et al., 1978). Cross-fostering, in which young are placed in the nest of another species, has been used to a limited extent, but efforts have met with poor results (Cade, 1980). Questions exist concerning behavior of young Peregrines raised by other species.

Release of adults has also been attempted experimentally. It requires release of a sexually mature adult in association with an existing territorial adult at a potential nest site, or a pair of adults during or just prior to the breeding season. The released adults must be in good physical condition and trained to capture suitable prey.

Use of augmentation of wild sites can only occur where at least a remnant population exists, and then only at sites where eggs or young exist. In California where fifty occupied territories are known, 80% of all releases can be accomplished by use of this technique. In 1982, 104 Peregrines were produced at Fort Collins, but eggs were laid at only seven wild sites within the release area. The maximum number placed with a pair of adults is four young, therefore the majority of the falcons were released by hacking. In the East no wild Peregrine reproduced until 1980, so all releases there were by hacking until that year.

The success of the release techniques is initially measured by numbers of young which not only fledge but which reach independence and disperse, usually about six weeks after initial flight. Approximately 75% of the young released by augmentation or by hacking have reached independence, but only 40% of the cross-fostered young have. An adequate number of adults have not yet been released to provide an estimate of the effectiveness of this technique. The final evaluation of release techniques is breeding of released birds. Many Peregrines released by hacking and augmentation are now occupying territories and reproducing normally (Table 2).

HABITAT

Releases can be made in historical or new areas. Historical habitat does not necessarily refer only to an historical nesting location. Instead it refers to the habitat type where the species was normally found to nest. New habitat refers to a habitat type not commonly associated with the species. Releases in new habitat, in the case of Peregrines, has occurred in cities or on towers located in marshes. By building artificial nest structures we have been able to provide new areas for breeding pairs. Peregrines historically used both cities and marsh areas for hunting during the non-breeding season. Both locations, especially the marshes, are occupied by tremendous numbers of prey and by few predators that may kill young falcons, such as exist at cliff sites.

Most Peregrines (70%) in the Eastern program have been released into new habitat. Reintroduction attempts at historical nest sites or in historical habitat were much less successful owing to predation by Great Horned Owls (Bubo virginianus) on young (Barclay, Cade, in press).

T a b l e 2

Summary of captive breeding, release and returning Falcons

| | Captive Breeding Hatched Reared | Released | | Known Adults and/or Sub-adults at Release Areas, 1982 ¹ | | | Estimated Number of Falcons, 1982 ² | |
|----------------|------------------------------------|--------------------|-----------------|---|------------------|--------------|---|--------------------|
| | | Attemp- ted | Success- ful | Total | Non-laying Pairs | Laying Pairs | Total | Two Years or Older |
| | | | | | | | | |
| Eastern | 649 (1973-1982) | 434 (1975-1982) | 337 | 27 | 4 | 6 | 160 | 58 |
| Rocky Mountain | 506 (1975-1982) | 329 (1976-1982) | 247 | 24 | 8 | 1 | 133 | 40 |
| California | 127 (1978-1982) | 87 (1978-1982) | 79 ³ | 9 | 2 | 2 | 36 | 12 |
| Total | 1282 | 850 | 663 | 60 | 14 | 9 | 329 | 110 |

¹ Numbers of returning falcons only represent individuals or pairs found defending a site and do not include other observations of non-territorial falcons.

² Figures based on a 50% mortality from independence to age one and 20% mortality every year thereafter.

³ Twelve released unbanded and all monitored only to fledging.

By contrast, in the Rocky Mountain program most releases (90%) have occurred in historical habitat. Ninety-five percent of the California releases have also been at historical nest sites. These figures reflect both the release techniques used and the fact that far more potentially suitable historical nesting habitat exists in the two western regions than in the East. Predation by owls also occurs in the West; however, Golden Eagles (Aquila chrysaetos) are a greater threat to hacked and augmented young, as well as to wild adults. About 20% of the sites occupied by adults with young in Colorado are lost to eagle and owl predation annually. Owing to predation the release success by hacking is greater than by augmentation in the Rocky Mountains. By locating hack sites in strategic places, predators can frequently be avoided. Towers located in marshes have been used in the Rocky Mountain region as have city release sites in California.

A disproportionately large number of released birds have been returning to release sites in new habitat. In part, this result may be explained by the limited number of potential nest sites and easier observation. The birds released at towers may also have a better survival rate with reduced predation and increased prey (Barclay, Cade, in prep.)

Captive-hatched and released Peregrines are returning to all regions. Six pairs laid eggs, and five reared young in the East in 1982 (one "pair" received assistance). Four other pairs were on territory and watched but did not lay. Other adult and sub-adult birds were found occupying territories. We feel a self-sustaining population of Peregrines will exist in the eastern release region within five years. Sixteen different falcons were identified at release sites in the Rocky Mountains in 1982. The first known breeding of a released falcon occurred there in 1980. Because of the vast expanse of large cliffs and potential nest sites throughout the mountains, locating returning birds is difficult, and restoration efforts will probably take longer than in the East. Eggshell thinning continues to occur in a portion of the Rocky Mountain population too. The California population has steadily increased. Released birds are present at some of the fifty occupied territories (Table 2).

DISCUSSION

The numbers and types of conservation strategies are limited only by the minds of the managers and scientists who work with living organisms. The example of the U.S. Endangered Species programs for the Peregrine Falcon show several approaches that have been applied to the same species under different circumstances. The value and importance of each depends on the situation and species under consideration. Pioneer efforts such as the Peregrine Falcon recovery programs are important in providing insight and confidence, so that other species can be managed. Because of the peregrine program, similar conservation efforts have begun with other species around the world. The California Condor (Gymnogyps californianus) is an example of a species for which captive breeding and hands-on management would not have been considered, were it not for the success of the peregrine programs.

No matter the conservation strategy pursued, the single and most significant factor affecting its success is the people doing the work. Great minds

can develop wonderful plans, and superb biologists can be hired, but unless excellence is carried down to the people holding the lowest position in the field or lab, the chances of success will be greatly diminished. One careless moment by a volunteer, student, or uncaring or untrained technician can cause a critical failure. Those involved must be skilled, highly motivated, and emotionally involved. Job unions or forty hour work weeks have no place in this field.

At no time in conservation history have so many organizations and people joined to "save" an endangered species as in the case of the Peregrine Falcon. To date most state and federal wildlife agencies, hundreds of conservation groups, numerous industries, and tens of thousands of private citizens have joined to assist with the Peregrine program. Neither The Peregrine Fund, as the nucleus of the effort, nor any other single group will be responsible for the recovery of the species. Only through cooperation has the effort succeeded thus far. That crucial element, cooperation, should be considered by all contemplating application of conservation strategies.

SUMMARY

Several management plans for threatened and endangered birds include reintroduction of birds into areas from which they have been recently extirpated or translocation of birds from their present range to areas from which they have been long absent or where they never previously occurred. Often reintroduction follows successful breeding in captivity, and translocation is used for species that are rapidly losing their present habitat. These conservation strategies are evaluated using case histories of the four Peregrine Falcon recovery programs in the United States of America as examples. Recommendations on guidelines for improving the success of these procedures are suggested.

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MANAGING BIRD POPULATIONS VERSUS MANAGING THEIR ECOSYSTEMS

Stanley A. Temple

University of Wisconsin, Madison, Wisconsin, USA

Many conservationists have emphasized the desirability of a synecological ecosystem-oriented solution rather than an autecological population-oriented solution to the problem of managing threatened species. Birds, however, owing to their mobility, spatial needs, population dynamics, and trophic positions in most communities, may not respond as well as other taxa to an ecosystem approach. Given the probable extent to which global ecosystem management will preserve remnants of threatened communities, we will still have to manage many birds on a population-by-population basis if they are to remain members of the preserved community.

PRIORITIES FOR EXTINCTION

Christoph Imboden

International Council for Bird Preservation,
Cambridge, UK

Because of their knowledge of processes in Nature, biologists generally know, from a strict ecological point of view, how conservation problems could best be solved. They are able to identify the basic priorities from the immediateness of a threat. Conservation in fact is not a problem for the biologist, but for the environmental technician, whose job it is to implement recommendations derived from biological knowledge, and for the politicians who will be responsible for economic and social consequences of any action.

While the I.C.B.P. through its vast network of experts is generally aware of the bird species and habitats most under threat, actual conservation action often bears little resemblance to the priority needs for conservation as identified by the pure biologists. In practice, the projects included in a conservation programme are selected more for their feasibility in a given political, economic and social climate, as well as their attractiveness to the general public, than for their relevance to conservation priorities.

Moreover, once included in a programme, projects may assume an individual momentum, supported by vested interests (whether scientific or otherwise), which can result in projects outliving their original objectives.

It must be accepted that an accelerated extinction rate of species, including birds, in the next few decades is inevitable. The problem then is for conservationists to recognize when this situation pertains for a particular species and to respond to it with "non-action", or perhaps by disguising action within a more acceptable project image. In reality, many conservation decisions and choices are made by default rather than in accordance with a previously determined priority structure: the converse of this process is the de facto establishment of "priorities for extinction".

Symposium

BIOGEOGRAPHY AND DEVELOPMENT OF AVIFAUNAS

Convener: J. BLONDEL, FRANCE

Co-convener: F. VUILLEUMIER, USA

BOCHENSKI Z.

THE DEVELOPMENT OF WESTERN PALAEARCTIC AVIFAUNAS FROM FOSSIL EVIDENCE

VUILLEUMIER F.

FOSSIL EVIDENCE ON THE DEVELOPMENT OF SOUTH AMERICAN AVIFAUNAS

MARTENS J.

SPECIATION AND THE DEVELOPMENT OF HIMALAYAN AVIFAUNAS

BLONDEL J.

HISTORICAL AND ECOLOGICAL EVIDENCE ON THE DEVELOPMENT OF MEDITERRANEAN AVIFAUNAS

THE DEVELOPMENT OF WESTERN PALAEARCTIC
AVIFAUNAS FROM FOSSIL EVIDENCE

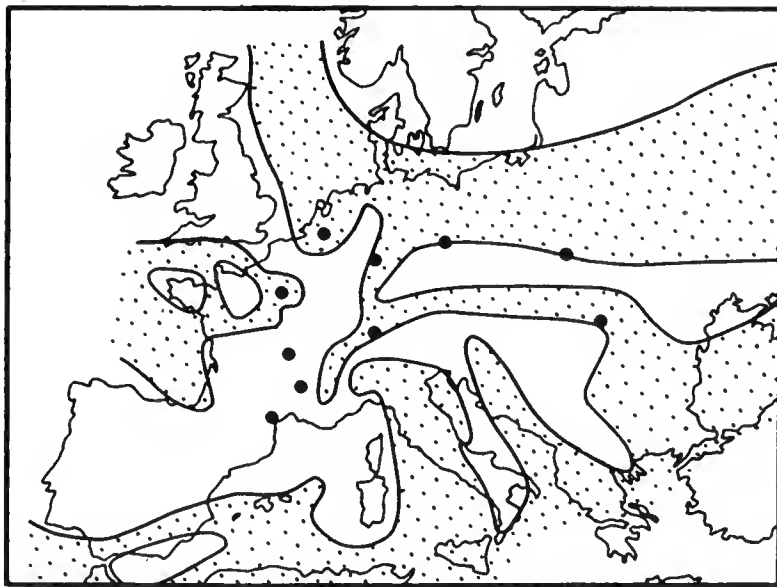
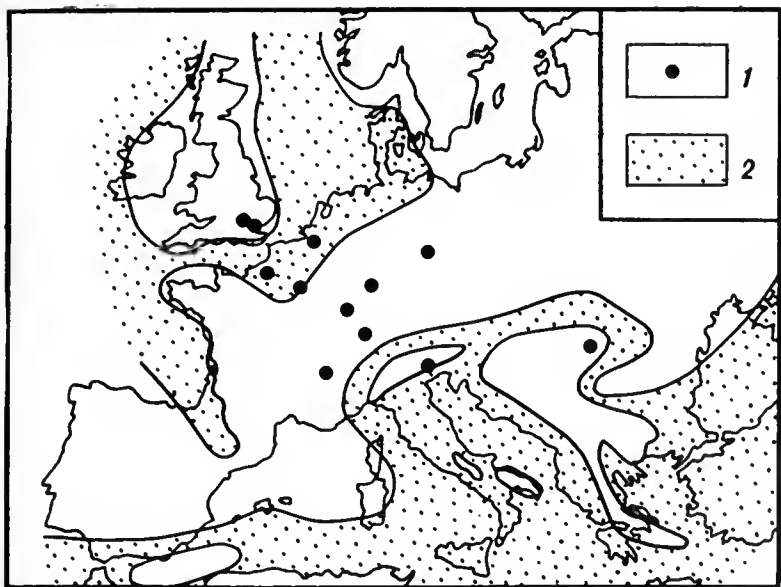
Zygmunt Bocheński

Institute of Systematic and Experimental Zoology,
Polish Academy of Sciences, Krakow, Poland

Whether we acknowledge Archaeopteryx to be the first link in the history of birds on Earth or regard it as a side evolutionary branch at the beginning of this history, the fact remains that the remains of this animal have been found in Bavaria in Europe and so the history of the birds of Europe, covering about 140 million years, is the longest. And again, irrespective of the fact whether, after Moreau (1966), we recognize "the median longevity of avian species" to be an imprecise concept of minor importance or, after Brodkorb (1971b), assume that it was about 500000 years, in the course of that long period the avifauna of the Western Palaearctic changed completely several times. Let us therefore try to epitomize our knowledge of the birds of this region against the background of geographic and geologic data. For the configuration of lands and seas was decidedly different in the past from that at present (Brinkmann, 1960; Pomerol, 1973).

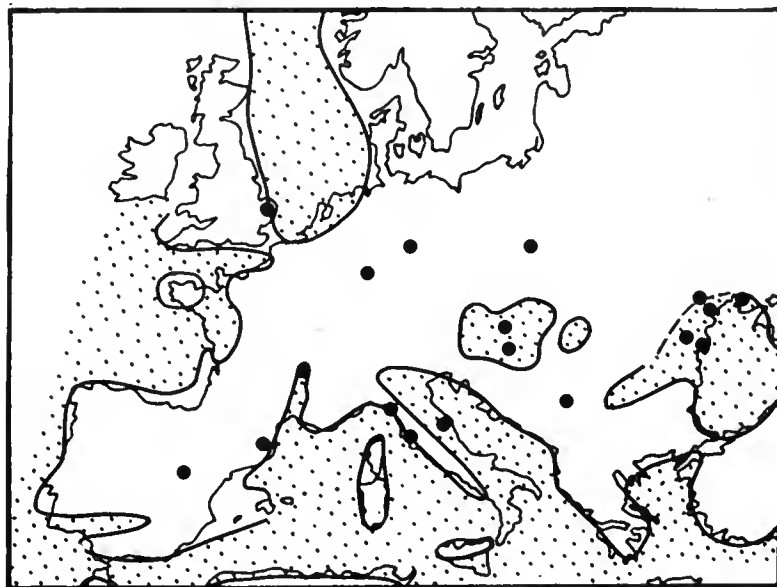
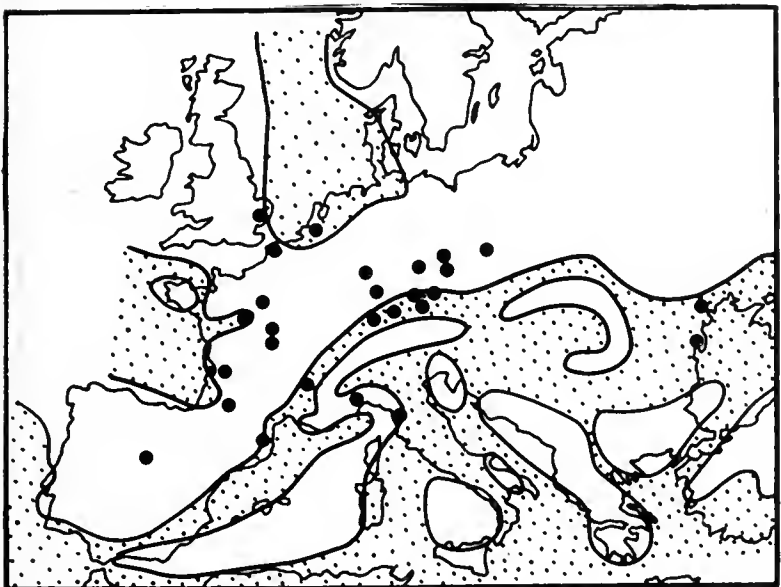
A total of 370 fossil bird species are known from the Western Palaearctic. The numbers of species occurring in particular periods of Earth history are given in Table 1. This table is based on the five-part Catalogue of Fossil Birds by Brodkorb (1963, 1964, 1967, 1971a, 1978), the studies published later and so not taken into account in it (Grigorescu, Kessler, 1977; Harrison, Walker, 1976; Jánosy, 1972, 1974, 1977, 1978, 1979, 1980, 1981; Kretzoi, 1977; 1977; Kurochkin, Ganea, 1972; Mlikovský, 1980; Mourer-Chauvire, 1975; Mourer-Chauvire et al., 1980; Paicheler et al., 1978; Švec, 1980, 1981; Tchernov, 1980) and some still unpublished materials from Poland and the USSR. These birds have been found in several dozen localities, the distribution of which is shown on the maps (Figs. 1-4). These being small-scale maps, a dot on them often represents several localities lying close to each other. Most of these localities appear to be situated in terrestrial sediments and a considerable part of the marine ones lie in the shore zone. One must also remember of the ranges of the Pleistocene glaciations, which sometimes left a thick layer of Quaternary deposits, frequently covering the older layers, to understand why there are hardly any Tertiary localities in Northern Europe, most of them being concentrated in the territory of France and GDR, FRG.

For the simplification of the picture I shall leave out the typical oceanic bird families from these considerations. Three main groups can be distinguished among the families whose members formed the fossil faunas of land birds. The first group consists of extinct families so far recorded only from the region under consideration. They begin with the Jurassic Archaeopterygidae, followed by the Cretaceous divers Elopterygidae, Palaeocene flamingos Saniornithidae and the Gastornithidae belonging to the rallids, Eocene Odontopterygidae, Aegialornithidae - the Eocene or Oligocene nightjars or Archaeotrogonidae recently raised to the rank of family by Mourer-Chauviré



F i g. 1. Eocene localities of fossil birds in Europe and the distribution of lands and seas in the Middle Eocene (Pomerol,1973). The seas are dotted; the broken line marks the eastern boundary of the area discussed in this paper

F i g. 2. Localities of fossil birds in Europe and the distribution of lands and seas in the Oligocene (Pomerol,1973). Symbols as in Fig.1



F i g. 3. Miocene localities of fossil birds in Europe and the distribution of lands and seas in the Middle Miocene (Pomerol,1973). Symbols as in Fig.1

F i g. 4. Localities of fossil birds in Europe and the distribution of lands and seas in the Pliocene (Pomerol,1973 - changed). Symbols as in Fig.1

T a b l e 1. Numbers of fossil bird species described from the Western Palaearctic in particular geological periods

| Period | Age in millions of years | Approximate number of species |
|---------------------------------|--------------------------|-------------------------------|
| Upper Jurassic | 135 | 2 |
| Cretaceous | 70 | 5 |
| Paleocene | 60 | 9 |
| Eocene | | 44 |
| Upper Eocene or Lower Oligocene | 40 | 45 |
| Oligocene | 25 | 20 |
| Miocene | 10 | 143 |
| Pliocene | 1.8 | 56 |
| Pleistocene | | 46 |

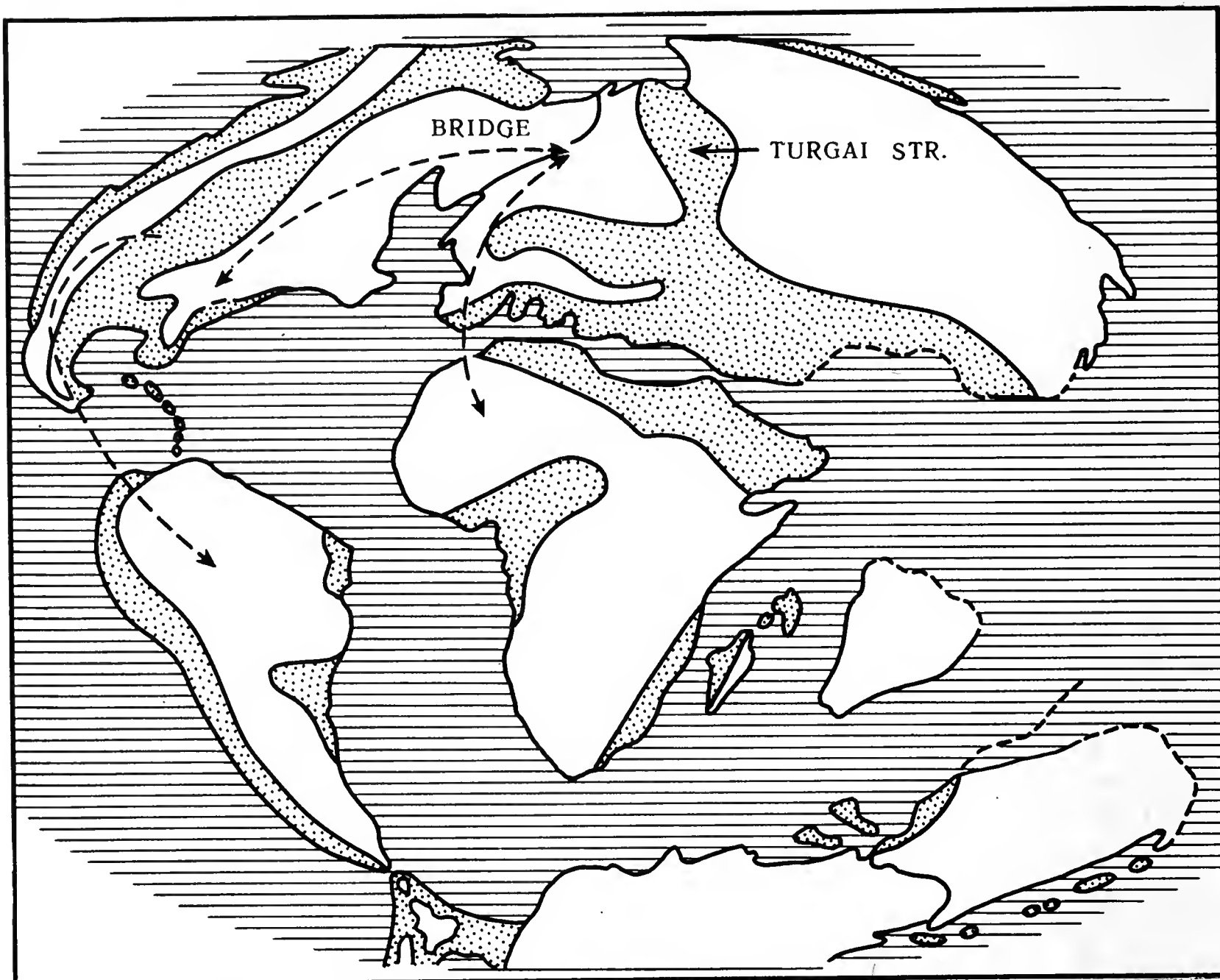
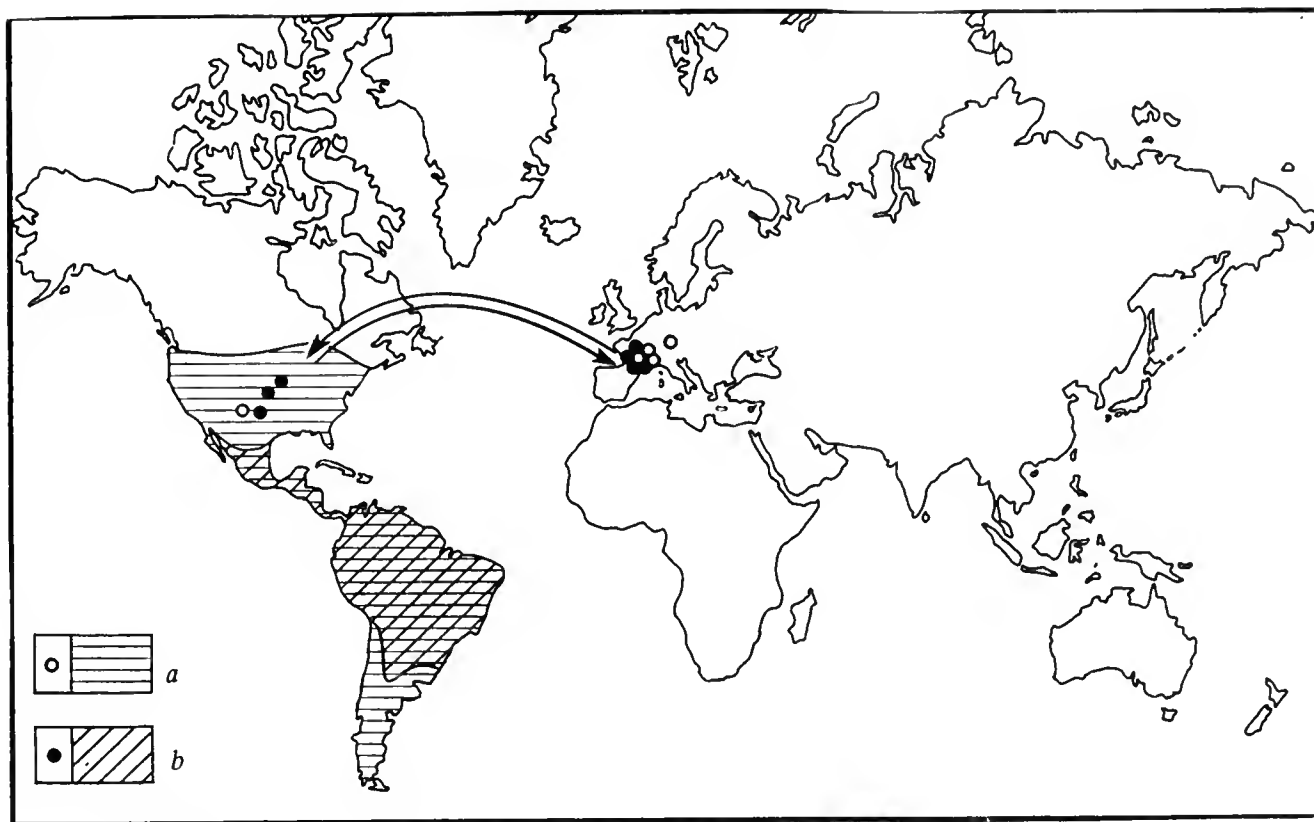


Fig. 5. North Atlantic land bridge connecting Europe and North America on the border between the Mesozoic and Caenozoic eras (after Rich, 1976, somewhat simplified). Arrows indicate directions of colonization

(1980), and from Oligocene ostriches Eleutherornithidae, from Miocene Pelagornithidae and Zygodactylidae belonging to the woodpeckers.

The second group includes the extinct families represented both in the Western Palaearctic and in other zoogeographical regions. And so the elephant birds of the family Aepyornithidae, which in historic times extinct in Madagascar, spread as far as Northern Africa, or to be exact Egypt and Libya, in the Eocene. The flamingos of the family Torotigidae in the Cretaceous and Paleolodidae in the Miocene are known from both Europe and North America. The occurrence of two families of the rallids - Idiornithidae and Diatrymidae - in the Early Tertiary in North America and in Europe is of particular interest. The presence of these flightless birds proves the existence of a land bridge across the North Atlantic (Fig. 5) from the Cretaceous to the Early Eocene (Kurten, 1967; Hoffstetter, 1981). We may conjecture that bridge was also used by the Phorusrhacidae, which are known from South American Oligocene to Pleistocene fossils and in which, after a revision carried out recently, Mourer-Chauviré (1981) included the genus Ameclinornis found in the phosphorites at Quercy in south-western France. And so there are many forms that the Old World has in common with America. On the other hand, only one extinct family described from East Asia, i.e. the cranes Ergilornithidae



F i g. 6. European (Eocene/Oligocene) and North American localities of the Cathartidae (a) and Cracidae (b) compared with their present distribution (Fisher, Peterson, 1964)

from the Oligocene deposits of Mongolia, is represented in the Upper Miocene fauna of the Ukraine and Moldavia (Kurochkin, 1981) by Urmiornis ukrainus. Naturally, the earlier exchange of faunas between Europe and the Siberian Plateau was prevented by the Turgai Strait, which formed a wide water zone east of the Urals, connecting the Arctic Ocean with the Tethys.

The third group was composed of the recent avian families represented on the fauna of the region concerned in the past epochs and now inhabiting exclusively even very remote areas. We meet with ostriches of the family Struthiidae in Europe in two periods very distant from each other, first a specimen of Eleutherornis found in Eocene layers in Switzerland and then about 40 million years younger members of the genus Struthio at several Lower Pliocene localities in the Ukraine and on Samos I. off the coast of Asia Minor. Represented by Struthio pannonicus, this genus still occurred in Hungary in the Lower Pleistocene. Members of the family Cathartidae, living till now in both Americas, occurred in western Europe in the Middle and Upper Eocene (Fig. 6). Cracraft and Rich (1972) put forward the hypothesis that on the Mesozoic-Cenozoic boundary these birds developed in the Old World - I think that the existence of the Turgai Str. allows the reduction of this area to Europe - and later reached America by the above-mentioned North-Atlantic land bridge. The Cracidae probably went the same way but the opposite direction; however, in Europe they did not live beyond the Lower Oligocene. Now, three other families have a similar distribution: they live in South America, in Africa south of the Sahara Desert and in south-eastern Asia, one of them also in Australia (Fig. 7). These are the Psittacidae recorded from the Lower Miocene of France, Trogonidae also from the Miocene of France and the Oligocene of Switzerland and Capitonidae from the Miocene of GDR, FRG. Only the palaeontological data concerning the parrots of the genera Archaeopsittacus from the Aquitanian of France and Conuropsis from the Upper Miocene of Nebraska

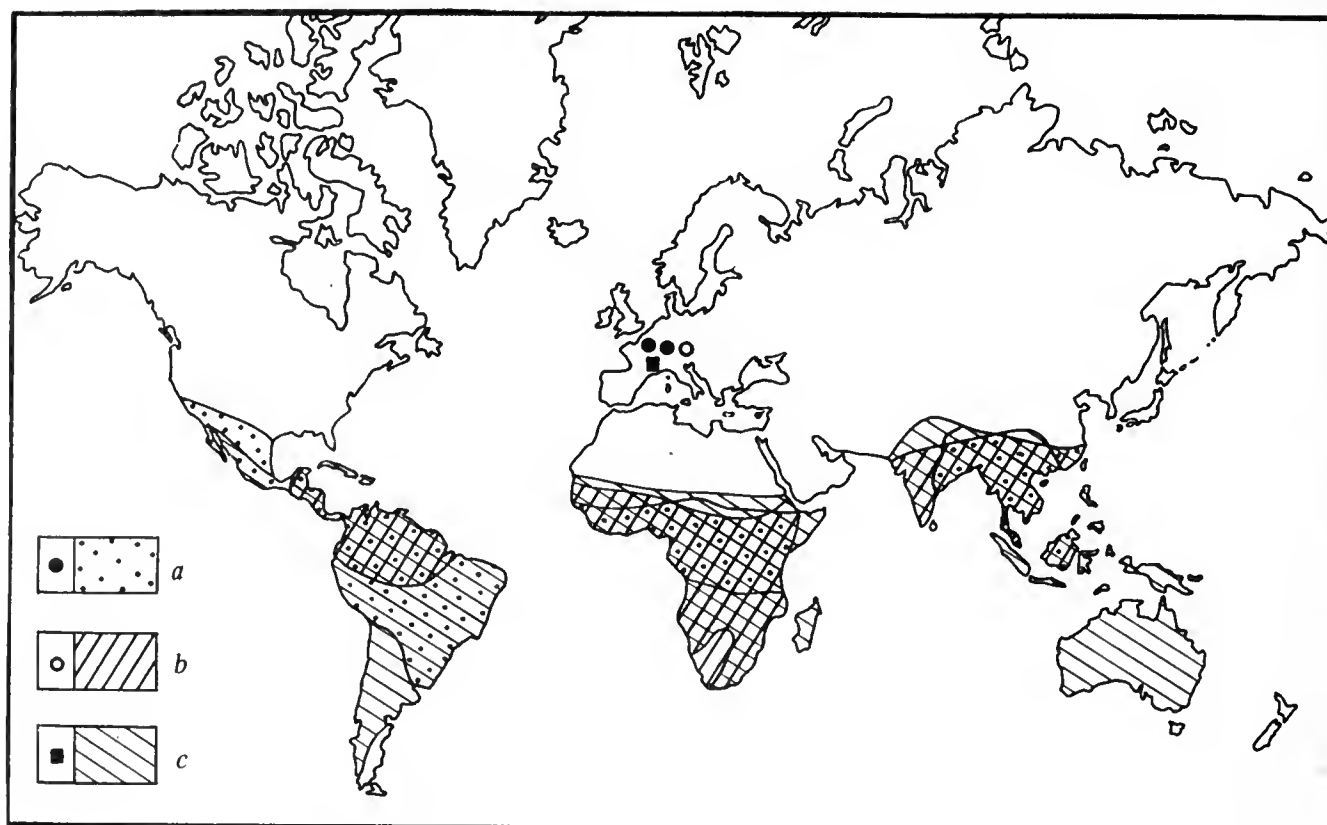


Fig. 7. Localities of the Trogonidae in the Oligocene and Miocene (according to Mourer-Chauviré, 1980) (a), Capitonidae (b) and Psittacidae (c) in the Miocene deposits of Europe compared with their present distribution (Fisher, Peterson, 1964)

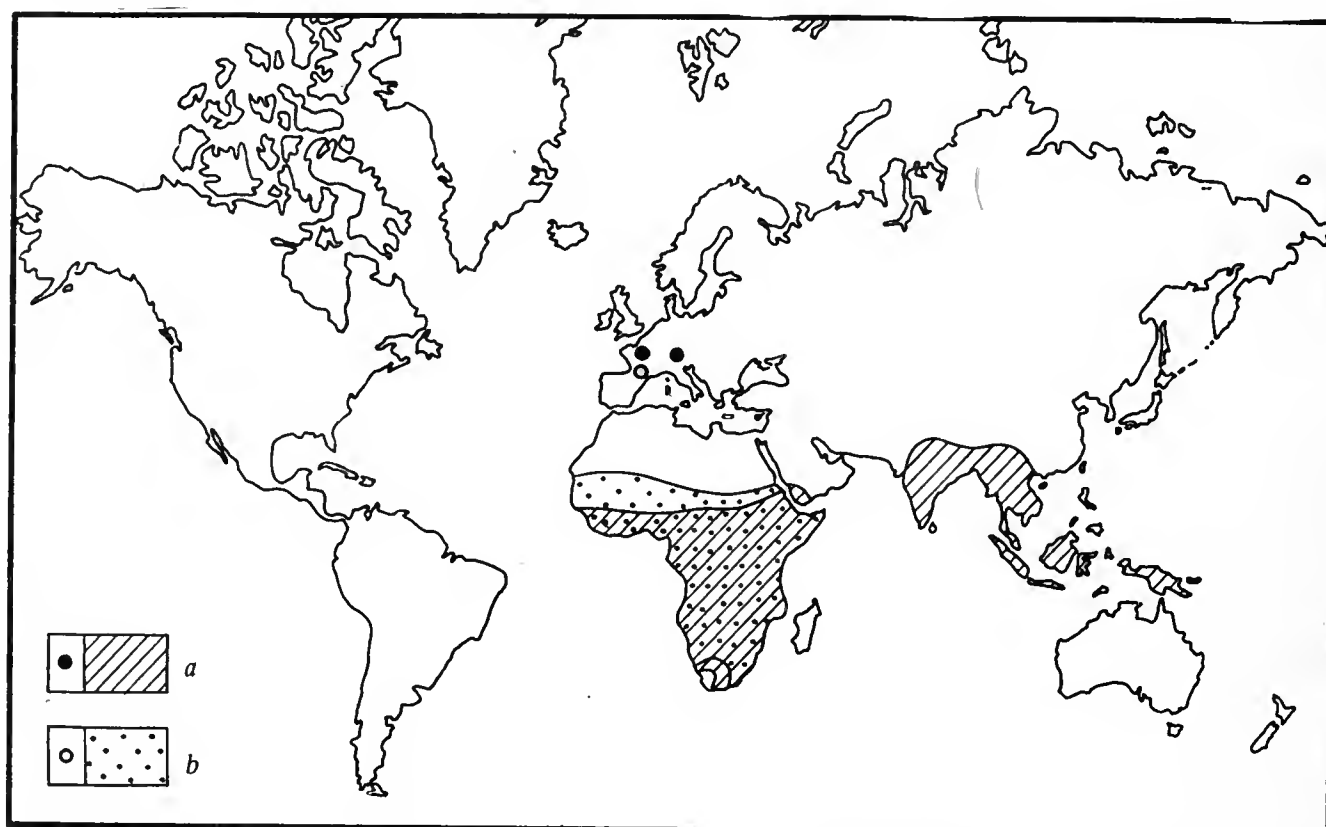


Fig. 8. Localities of the Bucerotidae (a) and Musophagidae (b) in the Eocene deposits of Europe compared with their present distribution (Fisher, Peterson, 1964)

ska may suggest that these birds, too, made use of the North Atlantic land bridge to colonize America.

The distance between the continent of Africa and Europe was never a "communication problem" for flying birds. Only for the last several thousand years the Sahara Desert has been an ecological barrier. Hence, it is much easier to explain the occurrence of the Bucerotidae and Musophagidae in the Eocene of Europe (Fig. 8) than that of the members of New-World faunas. Further elements, characteristic of the present fauna of the Ethiopian or the

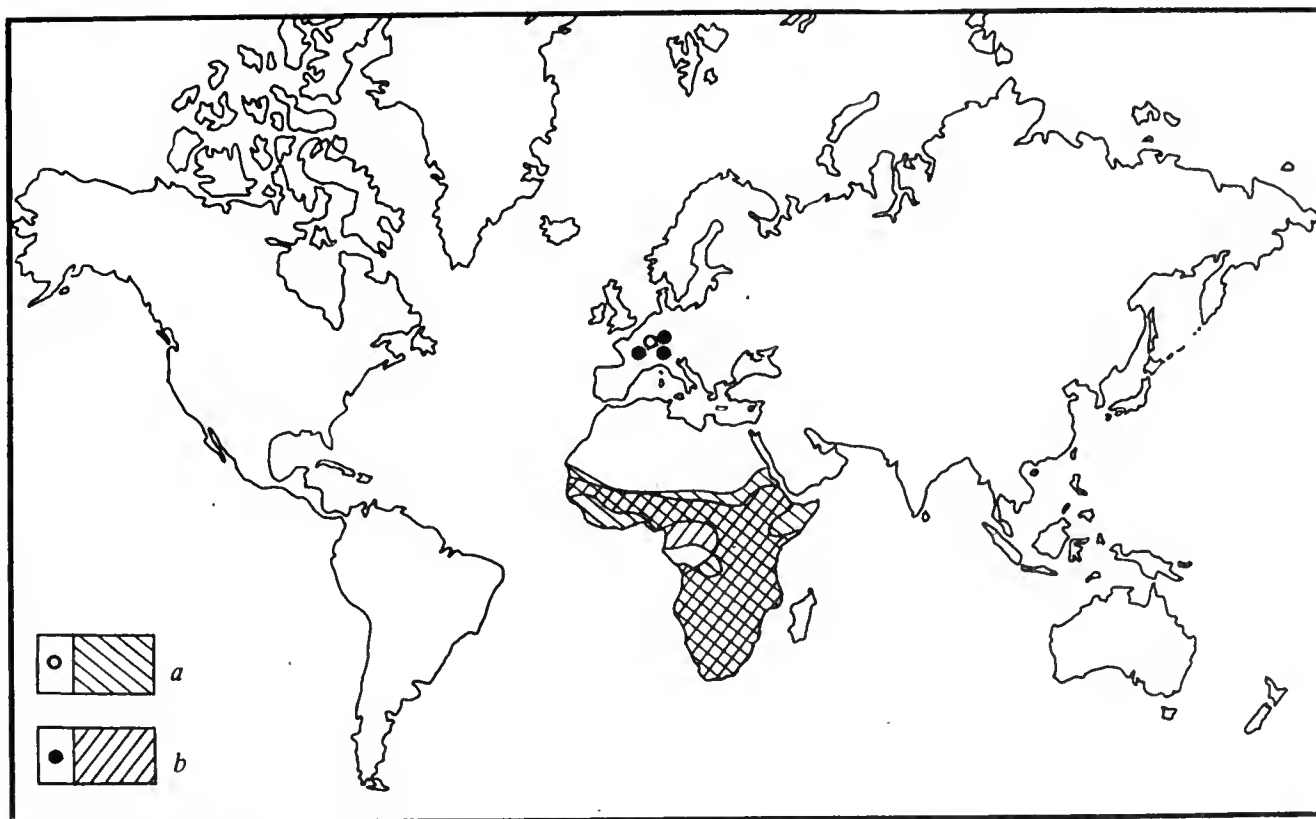


Fig. 9. Localities of the Sagittariidae (a) and Coliidae (b) in the Miocene deposits of Europe compared with their present distribution (Fisher, Peterson, 1964)

Ethiopian-Oriental region have been recorded from later, Miocene, deposits. Here belong the Secretary-bird, for whom Cracraft and Rich (1972) erected the new genus Amynoptylon, three species of Coliidae (Fig. 9) and some nondescript members of the Phoeniculidae and Eurylamidae. Subsequently, a member of the typical African family Numididae, the Guinea-fowl, unencountered before, appears here as late as the Upper Pleistocene and in Holocene archaeological excavations.

The development of the avian fauna of the Western Palaearctic can also be approached from another side, that is, from the standpoint of the present-day fauna. If the systematic division has been adopted from book by Harrison (1982), covering more or less the area with which we are here concerned, it will appear that now there occur members of 71 families in this territory. Their numbers in particular periods of Earth history are given in Table 2. The Gaviidae and Laridae, going back as far as the Palaeocene, are the oldest families. The picture very much resembling the present one did not appear until the Quaternary, when the fauna included 80% of the families that make up today's avian fauna of the Western Palaearctic. If we confined ourselves to Europe, this proportion would rise to 90%, for only the Hydrobatidae, Threskiornithidae, Phoenicopteridae, Haematopidae, Glareolidae and Paradoxornithidae were not represented in the fossil bird remains of the Quaternary of Europe. The oldest member of the present genus is Ardea piveteaui from the Upper Eocene of France, followed by Totanus edwardsii, two species of Pterocles, Bubo incertus and Asio henrici found in Upper Eocene or Lower Oligocene phosphorites of Quercy. Subsequently, in Oligocene deposits Sula ronzoni was found also in France, Anas basaltica in Czechoslovakia and Vanellus selysi in Belgium. A rapid quantitative leap in the Pleistocene is to a great extent connected with the occurrence of various families of the Passeriformes, which have been preserved extremely rarely in older deposits chiefly, as may be sup-

T a b l e 2. Numbers of present Western Palaearctic bird families represented in particular geological periods. Now the avian fauna of this region consists of 71 families

| Period | Number of families | % of the present fauna |
|---------------------------------|--------------------|------------------------|
| Paleocene | 2 | 2.82 |
| Eocene | 10 | 14.08 |
| Upper Eocene or Lower Oligocene | 11 | 15.49 |
| Oligocene | 10 | 14.08 |
| Miocene | 25 | 35.20 |
| Pliocene | 22 | 30.98 |
| Pleistocene | 57 | 80.27 |
| Holocene | 46 | 64.79 |
| | 58 | 81.69 |

posed, because of their flimsiness. The oldest passerine specimen known in the world has been described from the Upper Eocene of France as "Sitta cuvieri", which however, according to Brodkorb (1978) does not belong to the Sittidae. Next come the Oligocene birds from the Polish Carpathian flysch, but they have not been thoroughly studied yet.

If the Passeriformes have been omitted for their scarcity from the older deposits, there are 8 nonpasserine families the oldest remains of which have been found in the region under consideration in the Pliocene or even Pleistocene. Some of them, e.g. the Meropidae are not known from earlier deposits at all, others occurred earlier in North America and Asia. This indicates that these groups came to Europe from Asia in the Neogene or even at the beginning of the Quaternary. These are grebes: their oldest remains have been found in the Middle Oligocene of Kazakhstan (Kurochkin, 1976), from where they radiated to America in the Miocene and Europe in the Pliocene. The chronology of the finds of falcons, which are known from the Miocene in America, from the Lower Pliocene in Asia and from the Middle Pliocene in Europe clearly shows the direction of colonization. As regards the Tetraonidae, Cuculidae and Picidae, there are no data from Asia, though judging from their present distribution, they reached Europe from America that way, because the North-Atlantic land bridge had not existed for so long. It seems that the colonization of Europe by the Tetraonidae and Picidae may be associated with the development of the Eurasian forest zone. In a cooler phase of the preglacial period pine-spruce forests with deciduous trees, and so of the type of today's taiga, developed, which has also been shown for the Polish Lowlands (Stuchlik, 1975) and the Carpathians (Birkenmajer, Stuchlik, 1975), and both the Tetraonidae and Picidae include typical members of the taiga avian fauna (Stegman, 1931).

The Pleistocene is to be regarded as the period of formation of the present avian fauna of the western Palaearctic. It was being formed at a stormy times of climatic fluctuations connected with the successive glaciations of North and Central Europe, which were followed by equally drastic changes in the environment.

A huge majority of the fossil birds of the Lower and Middle Pleistocene

already belong to genera represented in the present fauna. These birds often differ slightly osteologically from the recent ones and therefore they are not always described as separate species; on account of their similarity, they are sometimes ranked with subspecies. In many cases they may be considered to be the ancestors of present species, e.g. Tetrao praeurogallus so far known from Hungary, Rumania and Poland and Tetrastes praebonasia, widely distributed in the Older Pleistocene, found in Hungary, Austria, Poland and France as well as Perdix palaeoperdix and Corvus antecorax from France or Dendrocopos praemedius from Hungary. Jánosy (1982) suggests that some of the birds described from the Older Pleistocene may have been the ancestors of twin species living in Europe at present. He mentions three forms, described by him, i.e. Lagopus atavus from Rebielice Królewskie in Poland as the ancestor of the Willow Grouse and Ptarmigan, Mergus connectus from Stranska Skala in Czechoslovakia as the ancestral form to the Goosander and Red-breasted Merganser and Strix intermedia described from Tarkö in Hungary, recorded besides from Austria, Czechoslovakia and France, which gave rise to the Tawny Owl and Ural Owl. Similarly, Falco antiquus, described from France by Mourer-Chauviré (1975), was the ancestor of the Gyrfalcon and Saker Falcon. Of many other species, such as, e.g., Milvus pygmaeus, Gallinula gigantea or Alauda jordanica described by Tchernov (1980) from Ubeidiya in the Jordan Valley it can only be said that they are closely related to the present-day species.

Writing about the development of the avian fauna of Europe, Jánosy (in prep.) emphasizes, as a very surprising fact, the contact of the ranges of the ancestors or close relatives of some Boreal forms in the Plio-Pleistocene, i.e. the Tetraonidae, represented by Tetrao conjugens and Tetrao macropus as well as Lagopus atavus and the Mediterranean francolins, namely, Francolinus capeki and Francolinus minor. Such a common occurrence of some members of the avian fauna of these two zoogeographical zones (although belonging to fairly remoted systematic groups) are still observed in the Upper Pleistocene. In that period we are concerned with modern species whose geographical distribution has changed much in the last 50 thousand years. This is illustrated on the map in Fig. 10, where the northern species are represented by Lagopus lagopus and Surnia ulula and the Mediterranean ones by Melanocorypha calandra and Pyrrhocorax graculus. The examples can be multiplied. And so Lagopus mutus extended as far as the Balkans (Bocheński, 1982), where it occurred together with Alectoris graeca. In Central Europe such northern forms as Falco columbarius, Eudromias morinellus or Numenius phaeopus were found together with the southern Aegypius monachus or Apus melba in upper Pleistocene materials (Bocheński, 1974).

The statement of a considerable rate at which changes in the distribution of particular species can take place is a platitude - we have observed them even if only during the last few decades. And although these changes occur continuously in various directions, it may be assumed that the general pattern of the present distribution of species in Europe developed at the beginning of the Holocene. Naturally, this was happening by degrees and not at the same time with all the species. Undoubtedly, the changes in the ranges were not the direct result of a warming of the climate in the Holocene, which may be

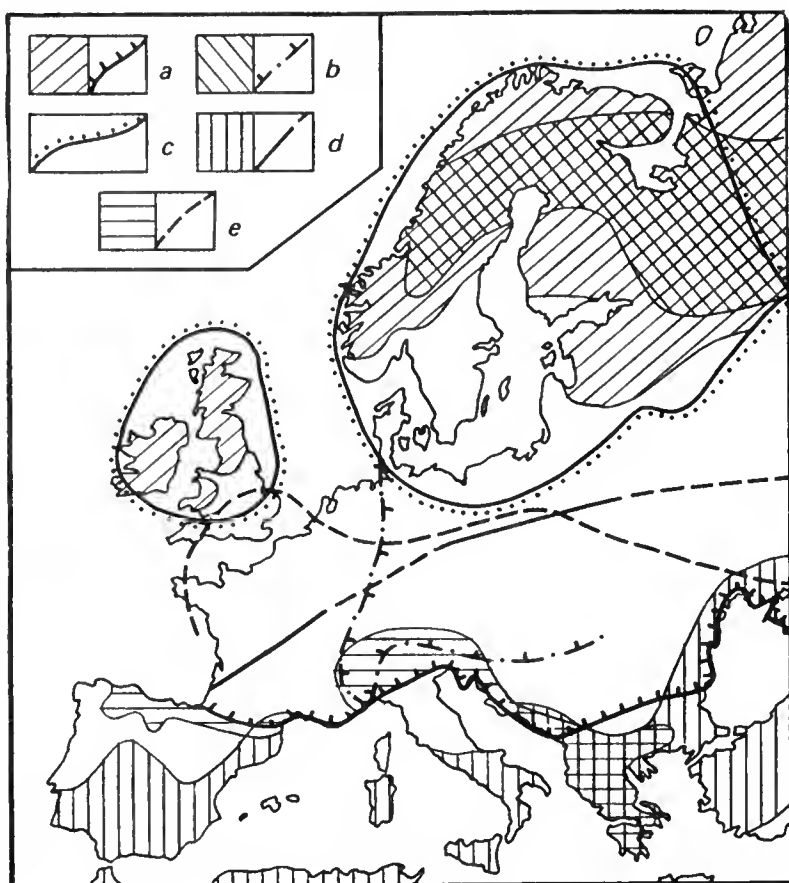


Fig. 10. The southern and northern boundaries of the distribution of selected bird in the Upper Pleistocene (Würm) compared with their present breeding areas (Bocheński, 1974, 1981; complementary data: Burčák-Abramovič, 1975; Cassoli, 1980; Malez, 1965, 1973; Mourer-Chauviré, 1975)

- a - Lagopus lagopus;
- b - Surnia ulula; c - maximum range of ice-sheet (Brinkmann, 1960);
- d - Melanocorypha calandra;
- e - Pyrrhocorax graculus

evidenced at least by the fact that the ranges of species overlapping in Central Europe during the last glaciation shifted apart, towards the north and the south. The withdrawals did not always agree with the changes in the optimum environmental conditions of given species. And so the Ptarmigan, which in the warm interstadials of the Würm occurred in forest environments, e.g. at Istalloskö in Hungary, where it was dominant (Jánossy, 1954), now is restricted to tundra habitats in the north and in mountains. Together with the Willow Grouse, it may have been worsted in competition by the increasingly numerous Black Grouse.

In overpopulated Europe man's activity could not have been unimportant to the distribution of birds in the last millenia and, notably, centuries, but this is the subject for another study.

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FOSSIL EVIDENCE ON THE DEVELOPMENT OF
SOUTH AMERICAN AVIFAUNAS

François Vuilleumier

Department of Ornithology, American Museum of Natural History,
Central Park West at 79th Street, New York 10024, USA

INTRODUCTION

Biogeographers have often discounted or largely ignored the avian fossil record in their reconstructions of zoogeographical patterns (e.g., Darlington, 1957: 238). The rationale for this attitude has usually been that the fossil record is too fragmentary to be truly helpful in zoogeographic reconstructions. According to this view, the few existing avian fossils may at best give indications about the presence of certain taxa at certain times in the past and at certain localities. Avian fossil remains are thus not sufficiently abundant (taxonomically or stratigraphically) to permit one to make deductions about the history of avifaunas. To quote Darlington (1957: 238): "Birds are a good example of the fact that, in zoogeography, a poor fossil record interpreted too literally is almost worse than no record at all."

As a neontologist interested in what fossil birds can tell us about the development of faunas, and contrarily to some widely held opinions among ornithologists, I have often been impressed with the fact that avian fossils are locally abundant. I have consequently wondered why so few qualitative or quantitative surveys of the fossil record have been attempted to check whether it might not yield valuable or new insights not obtainable from a study of Recent faunas alone. I thought that it would be appropriate for this Symposium to discuss some results of my survey of all fossil South American birds described until 1981 inclusive.

In this report I present a quantitative analysis of selected aspects of the development of South American avifaunas. Evidence is adduced to seek partial answers to the following three questions:

1. Does the fossil evidence bear out the classification of the South American avifauna into faunal elements of distinct geographical origins?
2. Do fossil birds provide one with any evidence on the temporal succession of avifaunas in South America?
3. Can Pleistocene avifaunas help us understand the development of Recent avifaunas?

MATERIALS AND ASSUMPTIONS

Materials. The materials for this paper come from a list of fossil South American landbirds - Procellariiformes, Spheniscidae (see Simpson, 1972, 1975), and seaducks (Tonni, 1979) were excluded. To compile this list I used Brodkorb (1963, 1964, 1967, 1971, 1978), Campbell (1976, 1979), Campbell and Tonni (1980), Cracraft (1970, 1971, 1981), Feduccia and McGrew (1974), Mones (1972), Olson (1977, 1981), Olson and Feduccia (1980), Pascual and Odreman Rivas (1971), Rich (1979), Tonni (1969, 1970a, 1970b, 1972, 1974, 1977a, 1977b, 1980), Tonni and Laza (1980), and Walker (1981).

For the geological epochs and ages I followed Simpson (1980, Chapter 3, his Tables 1 and 2), except that I considered the Divisaderan to be part of the Deseadan.

T a b l e 1. Synopsis of fossil South American Neornithes (seabirds excluded) complete to 1981, following Brodkorb's (1963, 1964, 1967, 1971, 1978) and Storer's (1971) systems

| Families | N Genera | | N Species | | Range in Time |
|-------------------|----------|------|-----------|------|-----------------------------|
| | Paleo. | Neo. | Paleo. | Neo. | |
| Tinamidae | 2 | 7 | 5 | 12 | Plio (Monte) - Recent |
| Rheidae | 2 | 2 | 4 | 2 | Mio (Santa) - Recent |
| Baptornithidae | 1 | - | 1 | - | Creta (Maes) |
| Podicipedidae | - | 2 | - | 2 | Late Plei - Recent |
| Phalacrocoracidae | - | 1 | - | 1 | Late Plei - Recent |
| Cladornithidae | 1 | - | 1 | - | Oligo (Desea) |
| Pelecanidae | 1 | - | 1 | - | Mio (Santa) - Recent |
| Presbyornithidae | 1 | - | 2 | - | Eo (Casa) |
| Phoenicopteridae | 1 | 1 | 1 | 1 | Oligo (Desea) - Recent |
| Threskiornithidae | 1 | 3 | 3 | 4 | Mio (Santa) - Recent |
| Ardeidae | - | 7 | 1 | 6 | Late Plei - Recent |
| Ciconiidae | 2 | 3 | 2 | 3 | Oligo (Desea) - Recent |
| Anatidae | 5 | 10 | 11 | 13 | Oligo (Desea) - Recent |
| Anhimidae | - | 2 | - | 2 | Late Plei - Recent |
| Cathartidae | 2 | 5 | 4 | 4 | Plio (Monte) - Recent |
| Teratornithidae | 1 | - | 1 | - | Plio (Huay) |
| Accipitridae | 5 | 8 | 7 | 9 | Oligo (Desea) - Recent |
| Falconidae | 2 | 4 | 3 | 8 | Mio (Santa) - Recent |
| Cracidae | 1 | 3 | 1 | 6 | Mio (Santa) - Recent |
| Phasianidae | - | 1 | - | 1 | Late Plei - Recent |
| Onychopterygidae | 1 | - | 1 | - | Eo (Casa) |
| Opisthocomidae | 1 | - | 1 | - | Mic (Fria) - Recent |
| Rallidae | 1 | 7 | 2 | 8 | Plei (Luja) - Recent |
| Aramidae | 2 | - | 2 | - | Oligo (Desea) - Recent |
| Cunampaiidae | 1 | - | 1 | - | Oligo (Desea) |
| Phororhacidae | 7 | - | 9 | - | Oligo (Desea) - Plio(Monte) |
| Psilopteridae | 6 | - | 10 | - | Oligo (Desea) - Plio (Huay) |
| Prophororhacidae | 1 | - | 3 | - | Plio (Huay-Monte) |
| Cariamidae | - | 2 | 1 | 2 | Plio (Monte) - Recent |
| Scolopacidae | 1 | 9 | 4 | 18 | Late Plei - Recent |
| Charadriidae | 1 | 5 | 3 | 7 | Late Plei - Recent |
| Recurvirostridae | - | 1 | - | 1 | Late Plei - Recent |
| Jacanidae | - | 1 | - | 1 | Late Plei - Recent |
| Burhinidae | - | 1 | - | 1 | Late Plei - Recent |
| Thinocoridae | - | 1 | 1 | 1 | Late Plei - Recent |
| Laridae | 1 | 2 | 2 | 4 | Plei (Luja) - Recent |
| Columbidae | - | 8 | - | 14 | Late Plei - Recent |
| Cuculidae | - | 3 | - | 3 | Late Plei - Recent |
| Psittacidae | - | 6 | 2 | 9 | Plei (Ense) - Recent |
| Strigidae | - | 5 | - | 6 | Late Plei - Recent |
| Tytonidae | - | 1 | - | 1 | Late Plei - Recent |

Table 1 (end)

| Families | N Genera | | N Species | | Range in Time | |
|------------------|----------|------|-----------|------|---------------|----------|
| | Paleo. | Neo. | Paleo. | Neo. | | |
| Caprimulgidae | - | 5 | 1 | 4 | Late Plei | - Recent |
| Nyctibiidae | - | 1 | - | 1 | Late Plei | - Recent |
| Apodidae | - | 1 | - | 1 | Late Plei | - Recent |
| Trochilidae | - | 1 | - | 1 | Late Plei | - Recent |
| Trogonidae | - | 1 | - | 1 | Late Plei | - Recent |
| Momotidae | - | 1 | - | 1 | Late Plei | - Recent |
| Bucconidae | - | 2 | - | 2 | Late Plei | - Recent |
| Ramphastidae | - | 1 | - | 2 | Late Plei | - Recent |
| Picidae | - | 3 | - | 5 | Late Plei | - Recent |
| Dendrocolaptidae | - | 2 | - | 2 | Late Plei | - Recent |
| Furnariidae | - | 1 | - | 1 | Plei (Ense) | - Recent |
| Formicariidae | - | 1 | - | 1 | Late Plei | - Recent |
| Hirundinidae | - | 1 | - | 1 | Late Plei | - Recent |
| Corvidae | - | 1 | - | 1 | Late Plei | - Recent |
| Mimidae | - | 1 | - | 1 | Late Plei | - Recent |
| Vireonidae | - | 1 | - | 1 | Late Plei | - Recent |
| Thraupidae | - | 1 | - | 1 | Late Plei | - Recent |
| Icteridae | - | 3 | - | 3 | Late Plei | - Recent |
| Emberizidae | - | 3 | 2 | 1 | Plei (Ense) | - Recent |

A b b r e v i a t i o n s: Plei - Pleistocene, Plio - Pliocene, Mio - Miocene, Oligo - Oligocene, Eo - Eocene, Creta - Cretaceous, Luj - Lujanian, Ense - Ensenadan, Monte - Montehermosan, Huay - Huayquerian, Fria - Friasian, Santa - Santacrucian, Desea - Deseadan, Casa - Casamayoran, Maes - Maestrichtian.

The fossil record of South American Neornithes includes 22 orders, 60 families, 193 genera, and 274 species. Table 1 lists all families and gives, for each, the number of genera and of species in the fossil record, and its range in time.

Assumptions. (1) I assume that the record of Cenozoic and Pleistocene South American birds represents a sample of the faunas that lived in South America in the past. This assumption is similar to that made by paleomammalogists for fossil mammalian faunas, in spite of the fact that the South American mammalian record is highly biased geographically and ecologically (see, e.g., Marshall et al., 1982: 1352). Since the same biases are found in the avian record as well, I conclude that my assumption is justified.

(2) I assume that a quantitative analysis of South American fossil birds may result in valid generalizations, even though some individual taxa may be presently misidentified and may be allocated to other taxa after further study. For example, even though extinct genus G₁ (belonging to extinct family F₁) may be eventually assigned to extinct genus G₂ or even to extinct family F₂, such a qualitative taxonomic shuffling is not likely to change the results of a quantitative analysis in terms of numbers and percentages of extinct taxa in the fauna being studied.

T a b l e 2. Faunal elements¹ of the fossil South American Avifauna²

1. Southern Hemisphere Element³

Tinamidae (Plio-Monte), Rheidae (Mio-Santa), Columbidae (Late Plei), Psittacidae (Plei-Ense), Opisthocomidae (Mio-Fria), Cuculidae (Late Plei), Cracidae (Mio-Santa), Phasianidae (Late Plei), Dendrocolaptidae (Late Plei), Furnariidae (Plei-Ense), Formicariidae (Late Plei).

2. Northern Element

Trochilidae (Late Plei), Momotidae (Late Plei), Cathartidae (Plio-Monte), Mimidae (Late Plei), Corvidae (Late Plei), Emberizidae (Plei-Ense), Fringillidae (Late Plei), Icteridae (Late Plei), Thraupidae (Late Plei), Vireonidae (Late Plei).

3. South American Element⁴

Anhimidae (Holo), Cariamidae (Plio-Monte), Phororhacoidea, 3 families (Oligo-Desea to Plio Monte), Aramidae (Oligo-Desea), Tinocoridae (Late Plei), Nyctibiidae (Late Plei), Bucconidae (Late Plei), Ramphastidae (Late Plei), Presbyornithidae (Eo-Casa), Cladornithidae (Oligo-Desea).

4. Unanalyzed Element⁵

Podicipedidae (Late Plei), Pelecanidae (Mio-Santa), Phalacrocoracidae (Late Plei), Ardeidae (Late Plei), Ciconiidae (Oligo-Desea), Threskiornithidae (Mio-Santa), Phoenicopteridae (Oligo-Desea), Anatidae (Oligo-Desea), Accipitridae (Oligo-Desea), Falconidae (Mio-Santa), Rallidae (Plei-Luja), Jacanidae (Late Plei), Charadriidae (Late Plei), Scolopacidae (Late Plei), Recurvirostridae (Late Plei), Burhinidae (Late Plei), Laridae (Plei-Luja), Strigidae (Late Plei), Caprimulgidae (Late Plei), Apodidae (Late Plei), Trogonidae (Late Plei), Picidae (Late Plei), Hirundinidae (Late Plei).

¹ Elements according to classification of Cracraft (1973: 519).

² Abbreviations as in Table 1.

³ Onychopterygidae (Eo-Casa) perhaps to be added to Southern Hemisphere Element.

⁴ Baptornithidae (Creta) and Cunampaiidae (Oligo-Desea) perhaps to be added to South American Element.

⁵ Teratornithidae (Plio-Huay) perhaps to be added to Unanalyzed Element (but could also be added to South American Element).

FAUNAL ELEMENTS

Mayr (1964) assigned South American families of birds to faunal elements of different geographical origins. Later Cracraft (1973) published a modified classification including the Southern Hemisphere, Northern, South American, and Unanalyzed Elements. Table 2 lists the families of fossil South American birds according to Cracraft's (1973) scheme and gives, for each family, the epoch(s) of its appearance in the South American fossil record.

The families placed in the Southern Hemisphere Elements range from the Miocene to the Late Pleistocene, whereas those in the South American Element

range from the Eocene to the Late Pleistocene. Thus South American families have a much greater temporal range and a considerably earlier fossil record than the families in the Southern Hemisphere Element. All families in the Southern Hemisphere Element have representatives living today, whereas 5 of the 12 families in the South American Element are extinct and ranged widely in the Cenozoic (Eocene to Pliocene). It would appear that a substantial component of the Tertiary South American fauna contained taxa that are now extinct and that have had important Cenozoic radiations. The question of whether the Southern Hemisphere Element and the South American Element are distinct and whether they are distinguishable on the basis of evidence from fossil birds (or from Recent birds for that matter) cannot be answered at present.

The Northern Element is made up of families with a Pliocene-Pleistocene fossil record in South America. This young age might suggest a relatively recent invasion of these families into South America and could be used to substantiate the definition of this element.

The Unanalyzed Element is the largest in number of families and includes only families with living representatives (ranging from the Oligocene to the Late Pleistocene). The heterogeneity and large size of this element, combined with the difficulty one encounters in trying to assign 4 extinct families (see footnotes 3, 4, and 5 to Table 2) to a given element, suggest either that the classification is not good, or that the fossil record is insufficient at present for allocation of some families to a faunal element, or both.

In view of several uncertainties mentioned above I conclude that it is premature to assign families of South American birds to faunal elements on the basis of fossil data. The fossil South American Avifauna is very diverse, and reflects a complex history on that continent. Study of this diversity, and reconstruction of that history on the basis of an analysis of putative faunal elements does not seem more than a crude and perhaps inaccurate procedure, which ought to be either dropped or else substantially improved.

FAUNAL SUCCESSION

Table 3 gives the total numbers of fossil families, genera and species, and numbers and percent of extinct families, genera and species in the various epochs represented in the fossil record. Table 3 shows that some families have survived from the Oligocene to the present but that in general Eocene-Pliocene faunas had a different familial composition (20-100% extinction) from Pleistocene ones (no extinction). At the genus level Eocene-Miocene faunas are composed entirely of extinct taxa. In the Pliocene appear genera that have survived until today (25% survival in the Montehermosan assemblage). But only the Late Pleistocene faunas are virtually identical to Recent ones in their generic composition (91-100% survival).

T a b l e 3. Numbers of families, Genera and Species (Passeriformes excluded) in the South American fossil record

| Fauna | Families | | | Genera | | | Species | | |
|--|------------|----------------|-----|------------|----------------|-----|------------|----------------|-----|
| | Total N | N Ex- tinct | % | Total N | N Ex- tinct | % | Total N | N Ex- tinct | % |
| Holocene (Venezuela) | 12 | 0 | 0 | 16 | 0 | 0 | 18 | 0 | 0 |
| Holocene (Argentina) | 13 | 0 | 0 | 18 | 0 | 0 | 18 | 0 | 0 |
| Late Pleistocene-Ho- locene (Brazil) | 41 | 0 | 0 | 78 | 1 | 1 | 95 | 2 | 2 |
| Late Pleistocene (SW Ecuador) | 15 | 0 | 0 | 37 | 3 | 8 | 51 | 10 | 20 |
| Late Pleistocene (NW Peru) | 22 | 0 | 0 | 67 | 6 | 9 | 87 | 22 | 25 |
| Pleistocene, Lujanian (Argentina) | 6 | 0 | 0 | 7 | 3 | 43 | 11 | 9 | 82 |
| Pleistocene, Ensenadan (Argentina) | 4 | 0 | 0 | 4 | 1 | 25 | 4 | 3 | 75 |
| Pliocene, Montehermo- san (Argentina) | 6 | 2 | 33 | 8 | 6 | 75 | 10 | 10 | 100 |
| Pliocene, Huayquerian (Argentina) | 4 | 4 | 100 | 5 | 5 | 100 | 5 | 5 | 100 |
| Miocene | 10 | 2 | 20 | 15 | 15 | 100 | 19 | 19 | 100 |
| Oligocene | 9 | 4 | 44 | 15 | 15 | 100 | 15 | 15 | 100 |
| Eocene | 2 | 2 | 100 | 2 | 2 | 100 | 3 | 3 | 100 |

A similar trend can be observed at the species level, with the difference that no Eocene-Pliocene species survived into the present. We can compare extinction in North and South American Pleistocene avifaunas because Selander (1965, his Table 2) gave extinction figures for North American avifaunas. After adding the Middle Pleistocene Haile avifauna from Florida (Ligon, 1965), with 16.7% extinct species, and including a revised figure for the Late Pleistocene Itchtucknee fauna of Florida (Campbell, 1980), with 10% extinct species, the average percentages of extinction are as follows: Late Pleistocene, 10%, Middle Pleistocene, 32%, and Early Pleistocene, 72%. Comparable extinction figures from South America (Table 3) are: Late Pleistocene, 20-25%, Middle to Early Pleistocene, 75-82%. The Middle to Late Pleistocene extinction rates appear somewhat higher in South America (see also Campbell, 1979: 141).

Table 4 shows how many genera of South American birds were also present in the North American fossil record. Other than Presbyornis and Anas, no South American genera are also present in North America until the Late Pleistocene, suggesting that South American faunas evolved in isolation during most of the Cenozoic. Whether or not the higher extinction rates in South

T a b l e 4. Numbers of Genera in the South American fossil record found in South America only or in both North and South America

| Epoch | Total N of Genera | N (%) of Genera in South Ame- rica Only | N (%) of Genera in Both North and South America |
|---|----------------------|---|---|
| Late Pleistocene (Peru) | 67 | 24 (36) | 43 (64) |
| Pleistocene (Lujanian and Ensenadan) | 11 | 10 (91) | 1 ¹ (9) |
| Pliocene | 11 | 11 (100) | 0 (0) |
| Miocene | 15 | 15 (100) | 0 (0) |
| Oligocene | 15 | 15 (100) | 0 (0) |
| Eocene | 2 | 1 (50) | 1 ² (50) |

¹ Anas.
² Presbyornis

America and the figures in Table 4 are, indeed, compatible with an interpretation made in terms of the Great American Interchange remains to be discovered after an analysis of individual taxa in the record of both continents.

PLEISTOCENE AVIFAUNAS

In Table 5 the Pleistocene faunas of South America are analyzed pairwise by means of the index $100 (C/N_i)$, where C is the number of taxa (genera or species) present in both faunas, and N_i is the number of taxa in the smaller fauna. The Late Pleistocene-Holocene faunas from Venezuela, Brazil, Ecuador, and Peru, taken two by two, share from 6 to 76% of their genera and of their species. Whereas the Venezuelan and Ecuadorian faunas share only 6% of their genera and species, those from Ecuador and Peru share as much as 76% of their genera and species. These differences are easily explained on geographical and ecological grounds. The similar Ecuadorian and Peruvian faunas both come from now desert areas and are geographically close to each other. The Venezuelan and Ecuadorian faunas are far apart, and differ in ecology, the Venezuelan one coming from more humid sites.

Argentine and Brazilian Late Pleistocene and Holocene avifaunas share 39% of their genera and species. Such a relatively high degree of faunal similarity is not surprising in view of the rather close geographical proximity of the sites, and of their being in relatively moist subtropical habitats.

It seems clear that the variation in degree of faunal similarity among the Pleistocene faunas of Table 5 represents an expression of the fact that the farther away any two faunas are in time or space, the lower their index of similarity, everything else being equal. Ecologically and geographically the patterns of Table 5 find close counterparts in Recent faunas.

T a b l e 5. Faunal similarity (in %) among South American fossil Avifaunas (Passeriformes excluded), right side of diagonal—species; left side of diagonal— genera

| | Holo. (Ven.) | Holo. (Arg.) | LP-Holo. (Brazil) | LP (Ecuad.) | LP (Peru) | Lujan. (Arg.) | Ensen. (Arg.) |
|--|-----------------|-----------------|----------------------|----------------|--------------|------------------|------------------|
| Holocene (Venezuela) | 100 | 6 | 39 | 6 | 39 | 0 | 0 |
| Holocene (Argentina) | 6 | 100 | 39 | 6 | 17 | 0 | 0 |
| Late Pleistocene- Holocene (Brazil) | 44 | 39 | 100 | 22 | 16 | 0 | 0 |
| Late Pleistocene (Ecuador) | 6 | 6 | 49 | 100 | 76 | 0 | 0 |
| Late Pleistocene (Peru) | 44 | 17 | 43 | 76 | 100 | 0 | 0 |
| Pleistocene-Lujanian (Argentina) | 0 | 11 | 29 | 0 | 1 | 100 | 0 |
| Pleistocene-Ensenadan (Argentina) | 0 | 6 | 25 | 1 | 1 | 0 | 100 |

According to Sick (1966: 359) the fossil species from Lagoa Santa (Late Pleistocene-Holocene of Brazil) represent a fauna very similar to that of today, but one which "appears to have nothing to do with the cerrado", a rather open vegetation formation. Nevertheless I note that of the 10 vicariant cerrado/humid tropical forest species pairs listed by Sick (1966), 5 (25%) occur in the fossil record, and 2 of these (10%) live in dense forest today. Such patterns of habitat selection may indicate a different climate in the Pleistocene-Holocene.

Many of the Late Pleistocene fossils from La Carolina (SW Ecuador) and Talará (NW Peru) belong to species that occur there today, including North American migrants, but Campbell (1982) in his discussion of the habitat preferences and possible origins of the fossil SW Ecuador-NW Peru avifaunas, pointed out that this area was considerably wetter in the late Pleistocene than today.

It seems clear that since Pleistocene faunas are so similar to Recent ones (Table 3) and vary as much as Recent ones do (Table 5), an understanding of the development of Recent faunas can only benefit from inclusion of Pleistocene fossil evidence (see Dementiev, 1960; Selander, 1965; Howell, 1969). However, changes in climate must be carefully taken into account.

SUMMARY AND CONCLUSIONS

Preliminary and partial answers to the three questions asked earlier are:

- (1) Fossil evidence does not fully bear out the classification of South American families into faunal elements. Much more work on Recent and fossil birds and fuller integration of both kinds of evidence will be necessary before we can hope to have a satisfactory stratification of South American birds into faunal elements. Moreover, the exercise appears of little heuris-

tic value and it might be best to turn to other kinds of zoogeographic analysis for study of development of avifaunas.

(2) Fossil birds offer evidence on faunal succession insofar as they tell us that Cenozoic faunas were very different from Pleistocene-Recent ones. Although the qualitative aspect of this result is not unexpected, the quantitative aspect is novel, and deserves much further study. Reconstructing Tertiary avifaunas without fully evaluating what is now known of the fossil record is clearly unsound.

(3) Pleistocene avifaunas can help us understand the development of Recent faunas if (a) detailed comparisons are made between the two (see Campbell, 1982, for a beginning in this direction), and (b) climatic changes are taken into consideration, since there is evidence that the climate was different in the Pleistocene at some of the sites where fossils have been found. A thorough integration of zoogeographic analysis based on Recent taxa with one based on Pleistocene ones should yield valuable information on faunal development.

ACKNOWLEDGMENTS

Richard Tedford and Mary LeCroy helped me during the preparation of this paper, which was typed by Mae Lackner and Jim Drobnick.

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SPECIATION AND THE DEVELOPMENT OF HIMALAYAN AVIFAUNAS¹

Jochen Martens

Institut für Zoologie, Saarstr. 21, D-6500 Mainz, FRG

INTRODUCTION

The Himalayas of South-East Asia extend for about 3000 km from the Indus bend in the north-west to the Tsangpo bend in the south-east. The area is inhabited by about 700 species of breeding birds. In Nepal alone in the central part of the mountain chain, there are 636 species, more than in North America. In this large number two important points emerge

1. Ecological - the different climatic conditions which vary according to latitude, longitude, aspect and altitude.

2. Zoogeographical - the Palaearctic and Oriental faunas meet on the southern slopes of the Himalayas. Representatives of both occur in the region.

Thus the high species diversity is not just the result of evolutionary processes, but also of a multitude of niches. It is largely an immigration fauna as is shown by the following:

- Some Himalayan birds occur over more extensive areas to the east west and partly to the north. From these an influx into the geologically young Himalayas took place;

- There are only 36 endemic species, about 5%, but several of these even extend beyond the Himalayan borders (Martens, 1981). Eight have relations in the Oriental, 25 in the Palaearctic and 1 in the Ethiopian region. But more taxonomic research is still needed on the endemic and closely related species.

Thus the Himalayan region by no means appears to be one rich in old endemics, nor one where intensive speciation has occurred influencing its own fauna and that of neighbouring areas.

GROUPS OF ENDEMIC SPECIES

The endemics of the Himalayas fall into several groups but not all species can be reliably classified:

a) Ancient relics with no closely related species. These comprise monotypic genera only and may originate from or even before the Himalayan uplift (Riplex, 1959): Catreus wallichii, Ophrysia superciliaris (Phasianidae), Callacanthus burtoni (Fringillidae).

b) Species without close relatives within their genera, in or outside the Himalayas: Capella nemoricola (Scolopacidae), Dendrocopos himalayensis, D. auriceps (Picidae), Garrulus lanceolatus (Corvidae), Phylloscopus tytleri, P. subviridis (Sylviidae).

c) Species with close relatives far outside the Himalayas: Phylloscopus occipitalis, P. lorentzii; Sitta cashmirensis (Sittidae).

d) Species with close relatives in or near the Himalayas, partly sympatric, partly allopatric: Tragopan melanocephala, T. satyra, T. temminckii (Pha-

¹Results of the Himalaya Expeditions of J. Martens, No.: xx. - No. xx: Senckenbergiana biol., 62 (xx/xx): xxx-xxx, 1983. - J.M. sponsored by Deutscher Akademischer Austauschdienst and Deutsche Forschungsgemeinschaft.

sianidae); species of the genera Aegithalos (Aegathilidae), Garrulax, Turdoides (Timaliidae), Carpodacus (Fringillidae), Phylloscopus.

e) This group does not comprise endemic species in a narrow sense, but in many cases species inhabiting large areas in northern Eurasia, as well as separated populations in the Himalayas. Normally considered as subspecies they give little insight into important behavioural differences and their possible meaning of speciation. They are of recent origin, referable to the Ice Age (Pleistocene). Such cases are best elucidated by acoustical analysis of their voices.

We have an exact idea of when and under which conditions the Himalayan endemics and their closest relatives evolved in only a few cases. This is true for the species of groups(a) and(b). Groups(c) and(d) are more favourable. Influences of glacial periods, causing regional reductions and thus initiating speciation processes, are quite often recognizable as causative agents. Group (d) illustrates recent evolutionary processes at the subspecific level, but acoustic characteristics show that differentiation has proceeded much further than previously accepted. Some populations may have been risen to the rank of species.

The following examples from(c) (d) and(e) have been quite well investigated.

SPECIES WITH CLOSE RELATIVES FAR OUTSIDE THE HIMALAYAS (1, 2)

Phylloscopus reguloides superspecies

The Himalayas are inhabited by 15 species of Phylloscopus out of some 30 species in the Palaearctic region. There are about 8-10 species locally everywhere in the mountain chain. This is the largest concentration of species within the range in the genus. Did most or at least many of the species evolve in the Himalayas? The relationships of the single species are not clear due to the great homogeneity of nearly all the species. In addition to the usual morphological characters I have used the voice as hints of relationships.

Relying on external morphology, the taxa occipitalis, reguloides, coronatus, davisoni and ijimae are thought to be closely related (Ticehurst, 1938; Williamson, 1976; Wolters, 1980). Of these only occipitalis and reguloides inhabit the Himalayas as well; occipitalis in the west and reguloides in the east. The remaining species live in East Siberia, East China and Japan (coronatus), South China and Indochina (davisoni) and in the Izu Islands (ijimae) (Fig. 1). Taxonomically they are classified differently by various authorities (Ticehurst, 1938; Vaurie, 1969; Voous, 1977; Wolters, 1980), but all seem to have acquired species level (Martens, 1980).

The close relationship of all five species is correct judging from their voices (Fig. 2). Syntax of territorial song as well as from elements show them to have many characters in common. This is also true for occipitalis and reguloides which are sympatric in the West Himalayas and thus their species status is proved. Only coronatus differs by its "clanking element" (fig. 2n-r) which normally does not occur in this species group (the song of davisoni is not yet known by sonagrams). Surprisingly we find the greatest conformity within those taxa whose species status was most disputed and which settle the most disjunct areas - occipitalis and ijimae, and not within

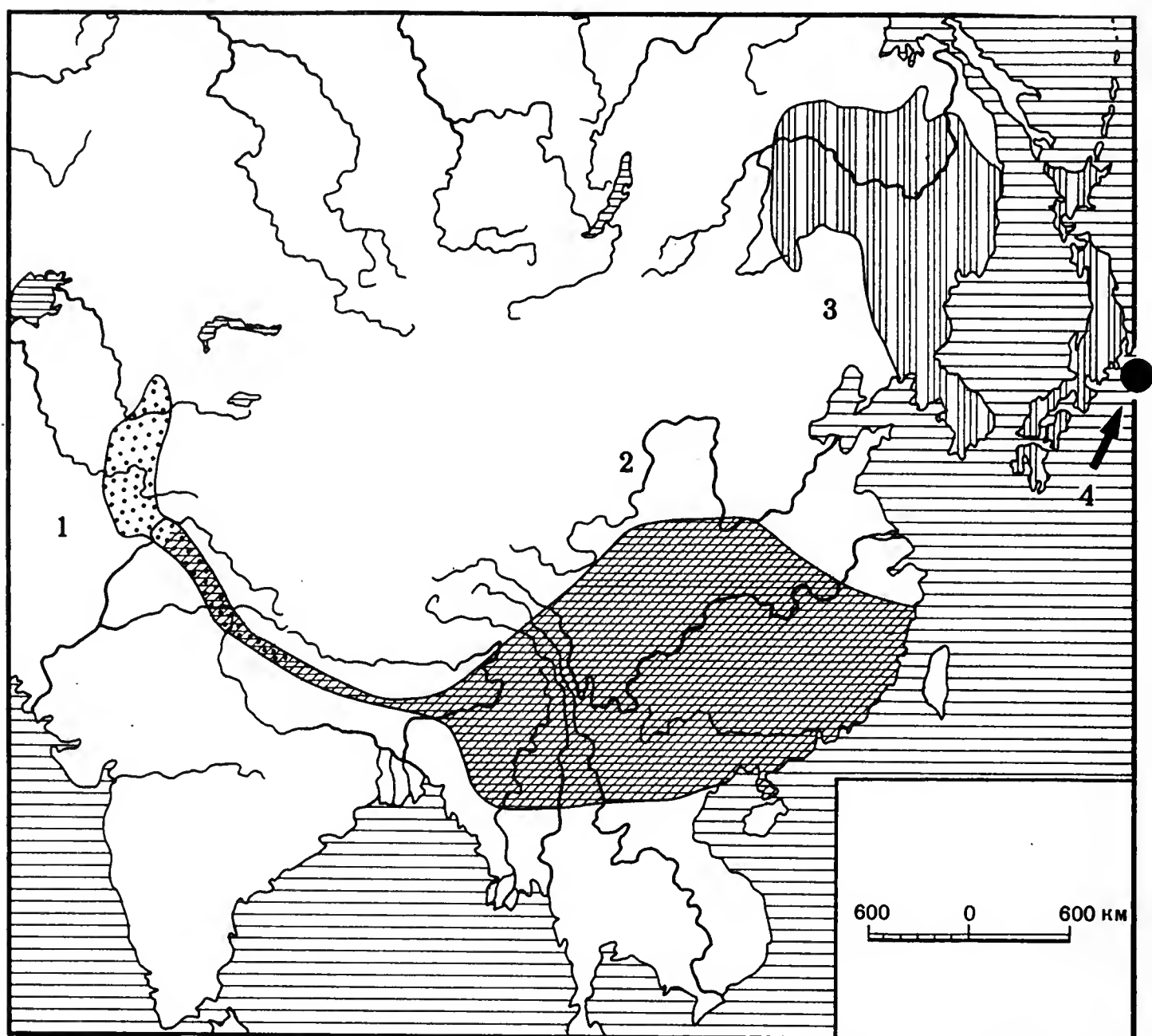


Fig. 1. Distribution of the species of the reguloides superspecies (except davisoni the area of which partly coincides with the area reguloides)

1 - occipitalis, 2 - reguloides, 3 - coronatus, 4 - ijima. After Martens (1960)

the neighbouring ijimae and coronatus from Japan (Martens, 1980) (see Fig. 1)

Interpretation: The species of the reguloides superspecies, confined to South-East Asia probably originated from a common ancestor, the area of which was split into relics during the Pleistocene. The single taxa evolved there and today it is still possible to recognize the refuge areas of occipitalis, reguloides, coronatus and ijimae, but not for davisoni which is largely sympatric with reguloides (Table 1). We still do not know if the five species developed simultaneously or during different periods of the Pleistocene. The Himalayas were of no importance during speciation and obviously occipitalis and reguloides immigrated when they had evolved.

Phylloscopus collybita - Phylloscopus lorenzii

This species ranges from North Africa to East Asia with isolated areas in the South Palaearctic mountain chains (Caucasus, Elburs, Karakoram/West Himalayas, Fig. 3). Two recognized subspecies groups are green forms in the West Palaearctic and brown ones in the East Palaearctic. In West Siberia fulvescens is considered a hybrid form of green and brown chiffchaffs (Williamson, 1976). In the Caucasus the brown lorenzii lives sympatrically with the green abietinus at 1800-2000 m approximately (Martens, 1982). It is provable that all green and brown subspecies are closely related. Besides the inherited

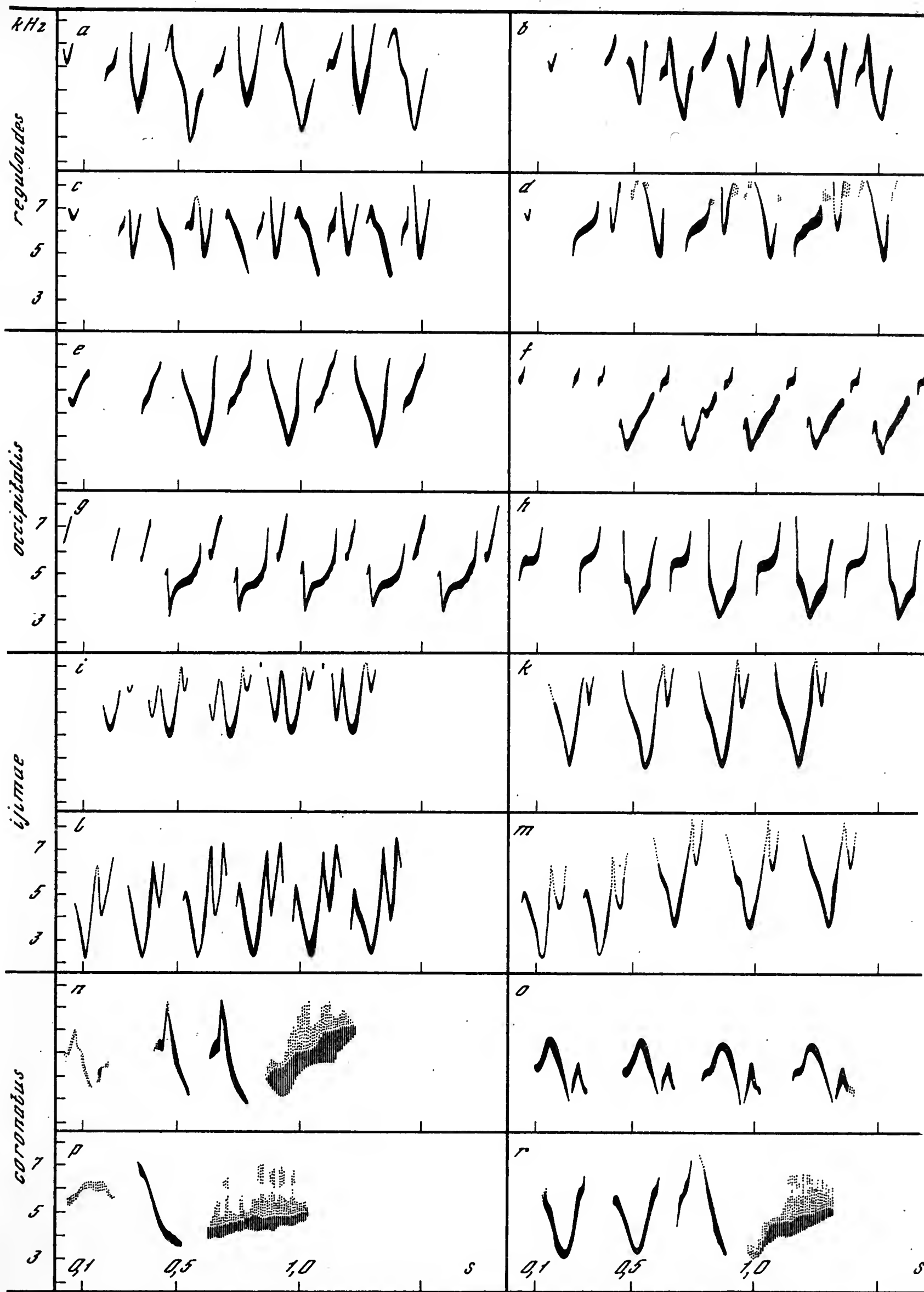
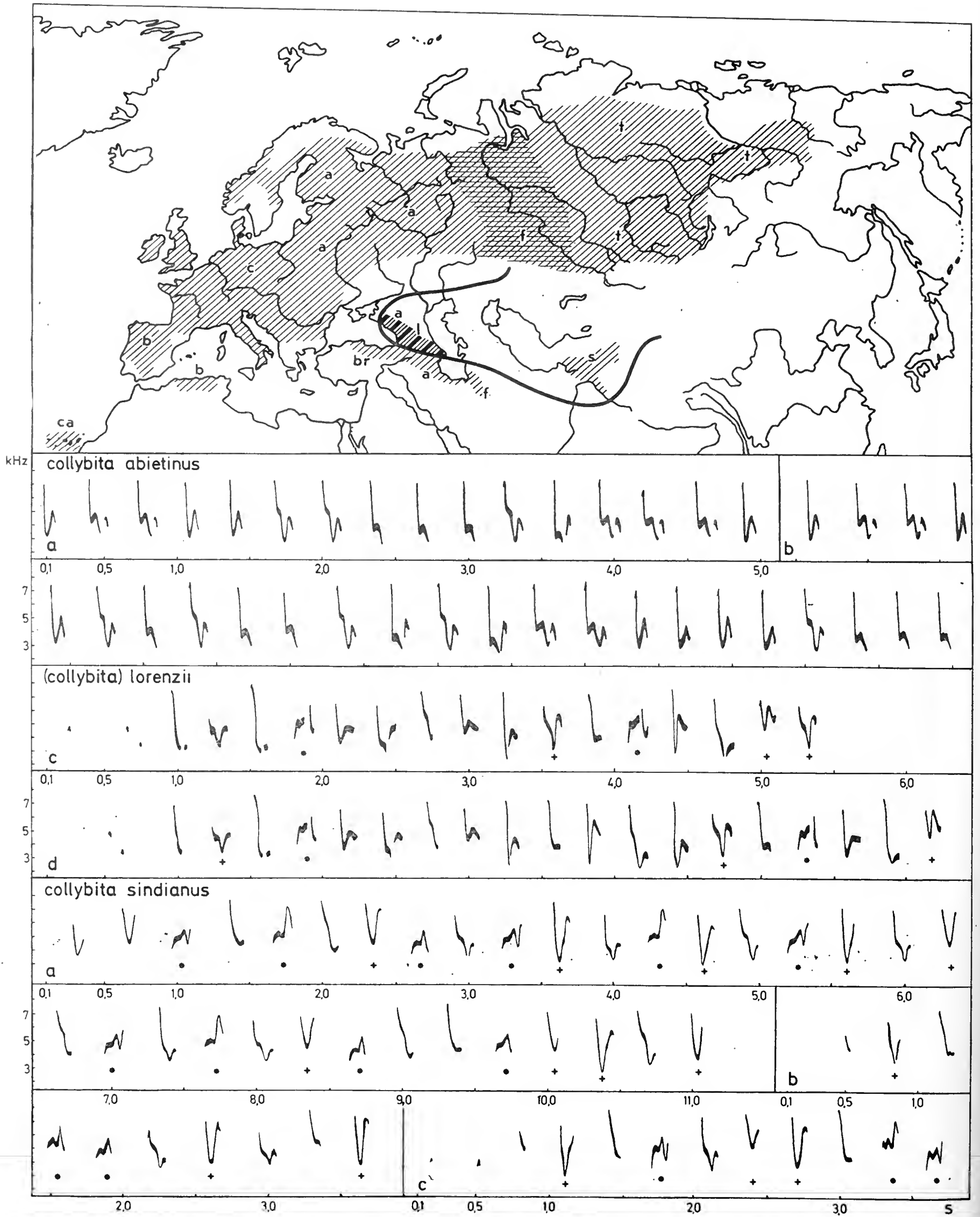


Fig. 2. Territorial song of species of the reguloides superspecies
a-d - reguloides (Nepal); e-h - occipitalis (India, Kashmir); i-m - ijimae (Izu Islands); n-r - coronatus (Japan) (after Martens, 1980)



T a b l e 1. Relations of taxa (species or subspecies) to possible forest refuges during Pleistocene as far as important for development of Himalayan avifaunas and recognizable from recent distribution

| Genus | Turkestan | Himalayan | Yunnan | Mongolian | Manchurian | Caucasian |
|---------------|------------|------------|------------|-----------|------------|-----------|
| Phylloscopus | occipita- | - | reguloi- | - | coronatus | - |
| | lis | | des | | | |
| Ph. collybita | sindianus | - | - | - | tristis | lorenzii |
| Ph. proregu- | - | simlaen- | chlorono- | ?proregu- | ?proregu- | - |
| lus | | sis | tus | lus | lus | |
| Parus | melano- | - | ater | ? | ? | ? |
| | lophus | | aemodius | | | |
| Parus | rufonucha- | rubidi- | rubidiven- | - | - | - |
| | lis | ventris | tris bea- | | | |
| | | rubidi- | vani | | | |
| | | ventris | | | | |
| Certhia | ?hodgsoni | ?hodgsoni; | khamensis | ? | ?macrodac- | ? |
| familiaris | | mandellii | | | tyla | |

colour characteristics, both groups are distinguished by their songs and these are passed on by learning to the next generation. Green subspecies utter the element type "falling-kneeled" and the brown ones in addition the "ascending-kneeled" (Fig. 3). The parameters of the song elements causing aggression in territorial males are more limited in green chiffchaffs than in brown ones. The multitude of element types leads to a richer and more complicated song in brown chiffchaffs. This is considered to be an apomorphic characteristic.

The archetype of all recent chiffchaff populations was coloured green in accordance with its closest relative, Ph. trochilus. It evolved in the West Palaearctic. The colour and acoustic characters of chiffchaffs changed when they settled in the East Palaearctic; brown pigments and "ascending-kneeled" elements occurred for the first time. Since one of the last glacial periods a distributional pattern resulted similar to the recent one; this was decisive for the speciation of the chiffchaffs; separated areas in the Mongolian or possibly Manchurian arboreal centre housed the recent tristis, the Turkestan one sindianus and the Caucasian lorenzii.

F i g. 3. Distribution and territorial songs of Phylloscopus collybita and Ph. lorenzii

Map with names of taxa, mainly subspecies: abietinus (a), brehmii (b), canariensis and exul (ca), collybita (c), fulvescens (f), lorenzii (l), sindianus (s), tristis (t). Brown chiffchaffs: tristis, sindianus, lorenzii; areas marked by fat line. Fulvescens is considered a hybrid of green (abietinus) and brown forms (tristis). - Song records are from the Caucasus (abietinus, lorenzii) and India, Ladakh (sindianus). - Stars below lorenzii and sindianus elements indicate "ascending-kneeled" elements. Elements with crosses do not release territorial behaviour in green chiffchaffs. For "falling-kneeled" elements see abietinus (after Martens, Hänel, 1981; Martens, 1982)

During post-glacial times only tristis was able to enlarge its area all over the Siberian taiga belt, lorenzii and sindianus remained stationary. In all three refuge areas separate evolutionary trends resulted, and today tristis is very different. The recent lorenzii and sindianus split their originally common area very late during Pleistocene times, judging from the similarity of their songs.

After secondary contact in West Siberia the green abietinus and brown tristis hybridized giving rise to fulvescens. Thus they are conspecific. But in the Caucasus the green abietinus infiltrated the brown relic lorenzii; they do not hybridize despite partial suitability of elements in their territorial songs (Martens, 1982; Fig.3). Brown and green forms behave as different species only in this place. Both morphological and acoustical similarity of sindianus (Himalayas/Karakoram) and lorenzii hint at conspecificity as well. but this cannot be proved.

Interpretation: Colour and acoustics which are passed on independently from each other by heredity and learning show that brown and green chiffchaffs are different in age and historical development. Among the brown forms in Asia lorenzii and sindianus are still very neatly confined to areas known as Pleistocene forest refuges. Only tristis was able to enlarge its area considerably in postglacial times. During separation sindianus and lorenzii changed their ecological demands. They adapted to high altitude biotopes and they live partly above the timber line. Green and brown chiffchaffs met only in one place where they behave as different species.

SPECIES WITH CLOSE RELATIVES IN OR NEAR THE HIMALAYAS,
PARTLY SYMPATRIC, PARTLY ALLOPATRIC (3, 4)

Parus ater - Parus melanolophus

P.ater inhabits a continuous area from N.Africa/Spain to East Siberia/Japan; in addition there are isolated areas in the South Palaearctic high mountains (Caucasus, Elburs, Zagros, Himalayas, Fig.4). The East Himalayan subspecies P.a.aemodius has a beige breast and belly, a crest and is small. In the West Himalayas and adjoining areas a very variant relative lives to which species status has been given; this is P.melanolophus in which the breast and belly are dark grey; the axillaries and under tailcoverts are chestnut coloured (Fig.4) and it is larger. It was believed that both Himalayan populations were allopatric with a distributional gap in the Central Himalayas (Vaurie, 1959), but I discovered a zone of contact and hybridisation in the Dhaulagiri-Massif in West Nepal (Diesselhorst, Martens, 1972). Both taxa exchange genes apparently without any behavioural incompatibility and inferiority of the hybrids. In the hybrid-zone the phenes change imperceptibly from aemodius-like to melanolophus-like types (Fig.5). The distance is only about 60 km from east to west. Among the melanolophus-like hybrids I discovered in only a very small part of the hybrid-zone (south slopes of Dhaulagiri, Dhorpatan, 3000 m) specimens representing a new type of pattern with a chestnut belly (Fig.4), very similar to Parus rubidiventris (see below). Also such hybrids pair freely with other colour types of hybrids (Martens, 1975).

Territorial songs of ater aemodius and melanolophus cannot be distinguish-

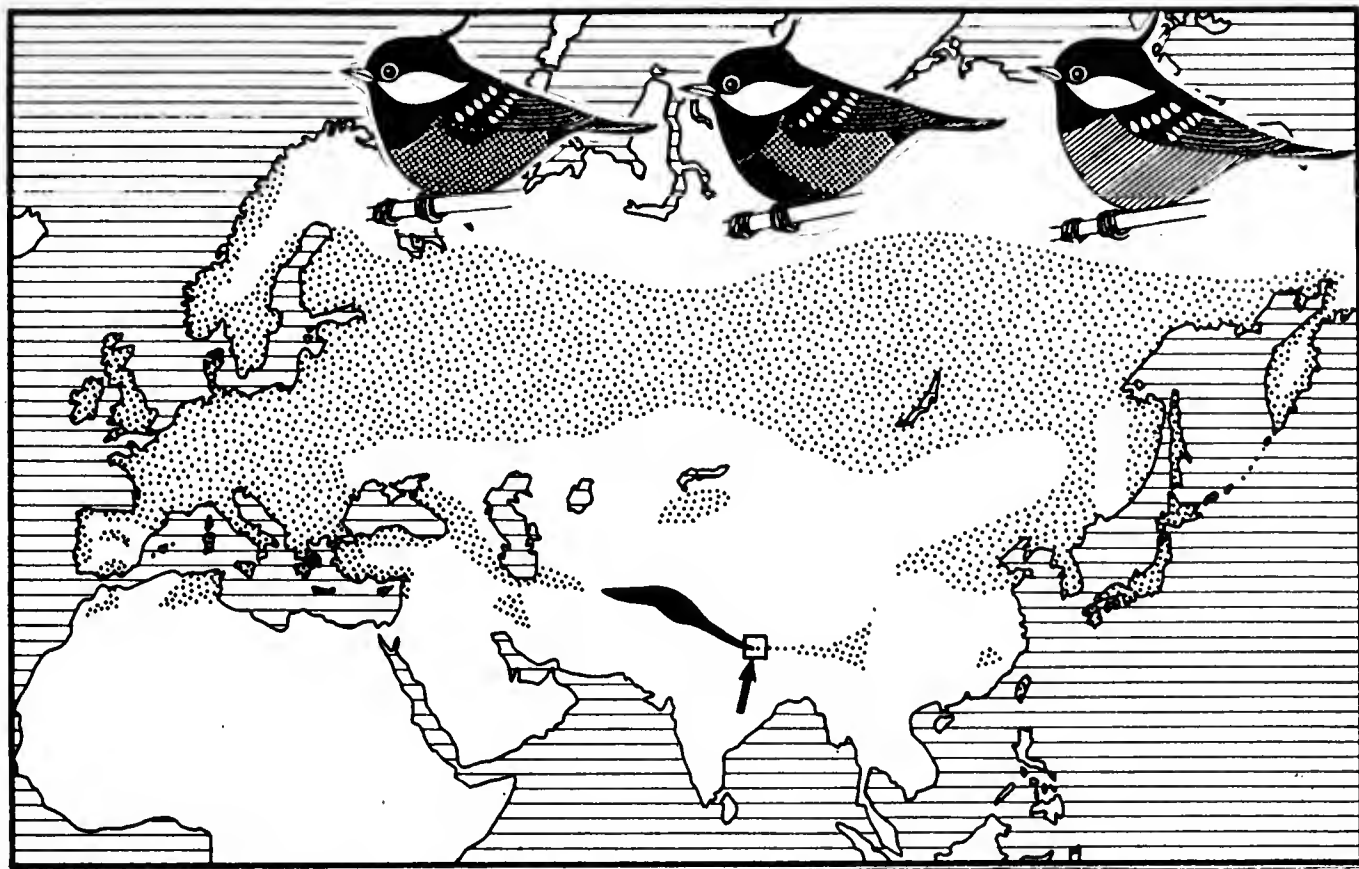


Fig. 4. Distribution of P.ater (hatched) and P.melanolophus (black) P.a.aemodius east of the arrow

Square-hybrid area (see Fig. 5). Figures from left to right: P.mélanolophus, chestnut bellied hybrid, P.ater aemodius (after Martens, 1975)

shed by the human ear. But single populations can be detected by sonagrams. P.a.aemodius has only descending elements of different quality, melanolophus may also use ascending ones. All partial populations of the hybrid belt use aemodius song.

Interpretation: P.a.aemodius and P.(a)melanolophus have their areas in secondary contact after they had spread from east and west into the Central Himalayas, respectively. They hybridize without any restriction despite strong differences in colour and pattern which evolved in different refuges east and west of the Himalayas. But voices and ecology remained unchanged. Distinct morphological characteristics probably do not indicate very different periods of separation in the aemodius melanolophus taxa group. Colours seem to be easily changeable in the Parus (Periparus) group.

Parus rufonuchalis - Parus rubidiventris

In the Himalayas and in the adjoining areas to east and west the great forms of Parus (Periparus) live - these are: rufonuchalis (West Himalayas and westwards), rubidiventris (Central Himalayas), and beavani (East Himalayas and eastwards, Fig. 6); rufonuchalis and beavani differ somewhat in size and pattern of grey and black on the breast and belly. Rubidiventris is similar to beavani, but differs in its chestnut belly pattern (see Fig.6).

Rufonuchalis and rubidiventris live sympatrically in West Nepal, thus they have to appear as two different species (Martens, 1971); their songs are very different (Fig.7). Songs of rubidiventris and beavani coincide and their distribution is allopatric; conspecificity is obvious. Hitherto it was believed that the Bhoté Kosi river in East Nepal formed the border between the two subspecies, no zone of intergradation being known (Martens, 1975). Recently

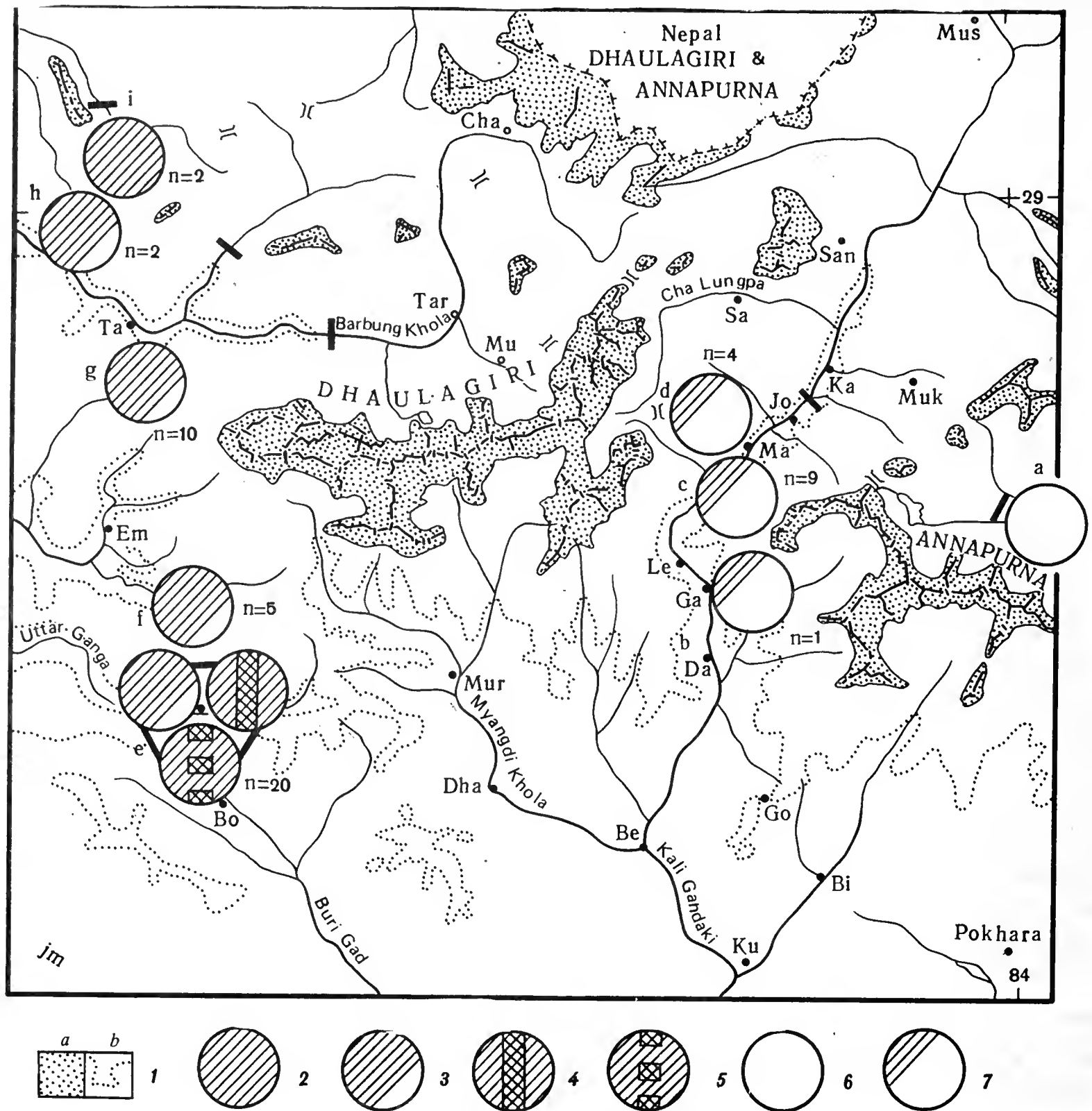


Fig. 5. Hybrid area of P.melanolophus and P.ater aemodius in the Dhaulagiri-Annapurna area, Nepal

In one place only (Dhorpatan, e) different types of hybrids occur 1a - areas more than 6000 m; 1b - area 3000 m; 2 - melanolophus; 3 - similar melanolophus; 4 - chestnut-bellied hybrid; 5 - similar chestnut-bellied hybrid; 6 - ater aemodius; 7 - ater aemodius melanolophus. After Martens (1975)

beavani was observed in Langtang Valley within the area of rubidiventris (Borradaile et al., 1977). It is not known if hybridization occurs. Three P.rubidiventris collected south of Langtang show no trace of hybridization (Martens, 1975).

Interpretation: The three taxa are closely related and stem from a common archetype but differ in age. The archetype may have been formerly distributed in the Siberian Taiga belt. Its area was reduced during Pleistocene, a population split off early and developed in the Turkestan refuge to the recent rufonuchalis. Another relic population represented the precursor of the recent beavani/rubidiventris group. It evolved east of the Himalayas in the

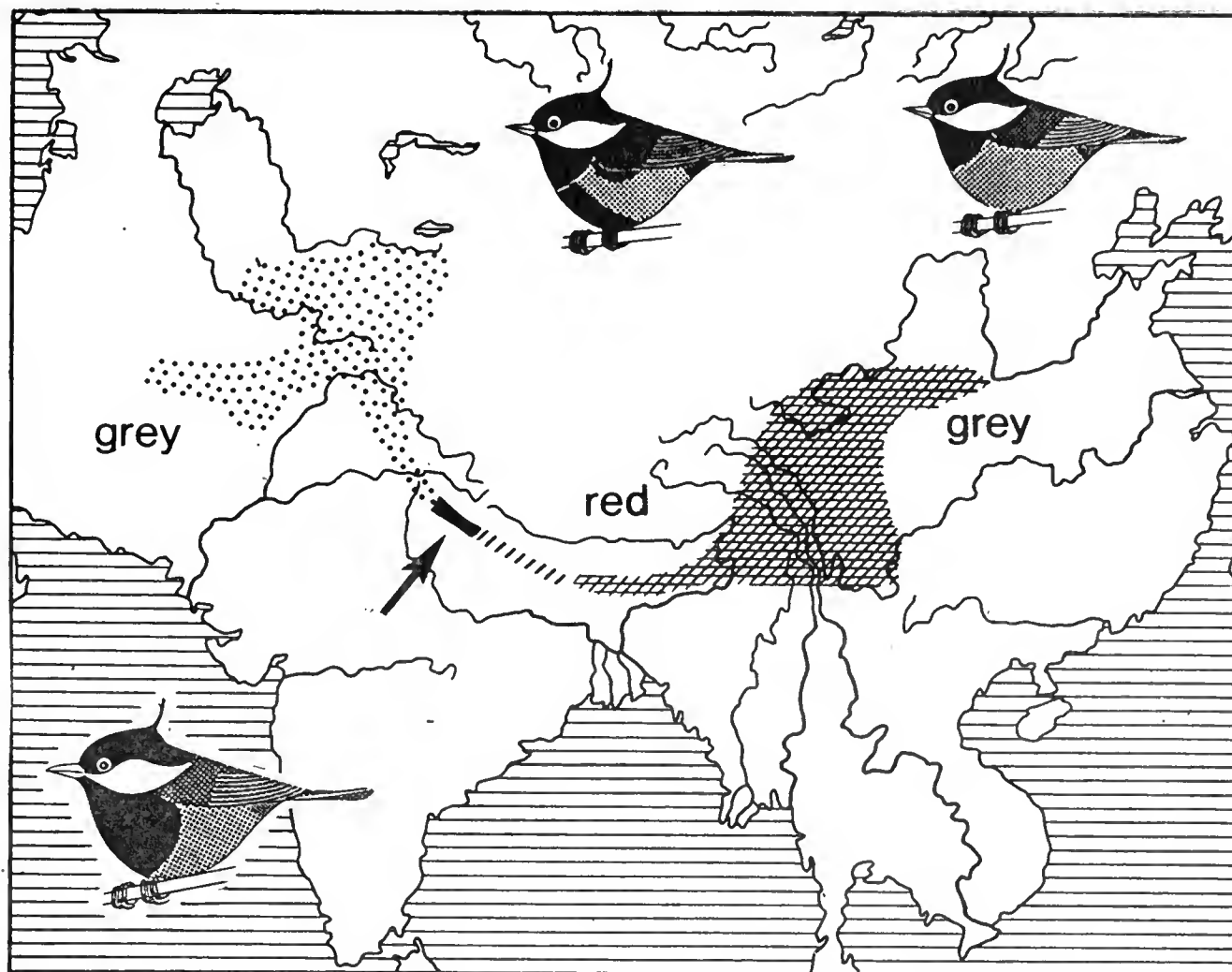


Fig. 6. Distribution of Parus rufonuchalis (west), P.rubidiventris rubidiventris (centre) and P.r.beavani (east)

Black area (arrow): sympatric occurrence of rufonuchalis and r.rubidiventris. "Grey" and "red" indicate colour of belly. Figures correspond with areas (after Martens, 1975)

Hiver Gorge Country and then spread into the eastern parts of the mountains. A small population of it was obviously isolated in later glacial period in the Central Himalayas; this evolved into the recent rubidiventris with a distinct colour pattern (Fig.6). This shows clearly that the Himalayas harboured a separate population and thus acted as a refuge. During this period there were closely related but isolated populations - beavani in the East and rufonuchalis in the West of the Himalayas. Secondary contact of the three populations was established only in post-glacial times.

SPECIES LARGELY DISTRIBUTED IN THE PALAEARCTIC WITH SEPARATED POPULATIONS IN THE HIMALAYAS (5, 6)

Certhia familiaris

This species inhabits a great area from West Europe to Japan. In addition there are isolated areas in the South Palaeartic high mountains the one in the Himalayas being the largest. All Eurasian populations are considered conspecific in their morphological characters in the same way as in the American tree-creepers. Their songs differ markedly from the European populations (Thielcke, 1962; Baptista, Johnson, 1982) and several authors give them species status.

Again the songs and calls of Nepal populations are very different (Fig.8). In field experiments C.f.mandellii (Nepal) does not react to the song of C.f.macrodactyla of Central Europe. In addition to differences in song struc-

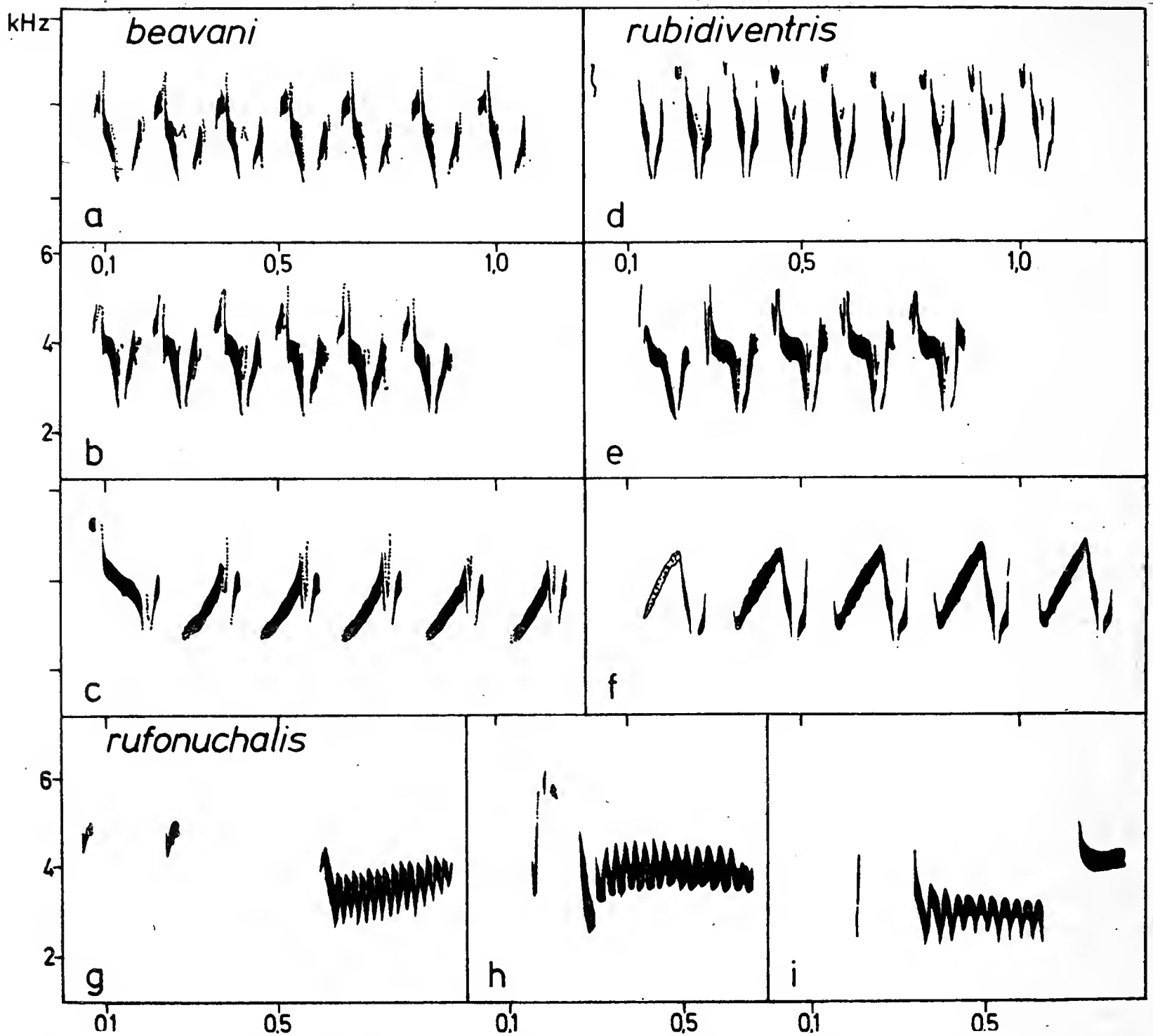


Fig. 7. Territorial songs of Parus rubidiventris beavani (a-c), P.r.rubidiventris (d-f) and P.rufonuchalis (g-i); all records from Nepal. After Martens (1975)

ture the calls also differ. Homologous calls of mandellii and macrodactyla differ in fine structure and meaning and in both cases can be traced back from elements of the territorial song. To indicate rivalry and long distance contact, mandelli consistently uses a strong frequency modulated "srieh" and rarely a smooth "zieh" for rivalry. Macrodactyla utters "zieh" in rivalry and the structurally simpler "srieh" for long distance contact. Both types of typically structured calls occur also as song elements of mandellii and macrodactyla respectively.

Interpretation: During one of the glacial periods a tree-creeper spread into the Himalayas and the east marginal mountains. There it differentiated into three subspecies - hodgsoni, mandellii and khamensis, distinct in their colouration and voice, though only mandellii's voice is known hitherto. As a result "understanding" by voice and calls between representatives of the distributional areas Europe - Himalaya seems to be impossible and sonagrams reveal the marked differences also (Martens, 1981b).

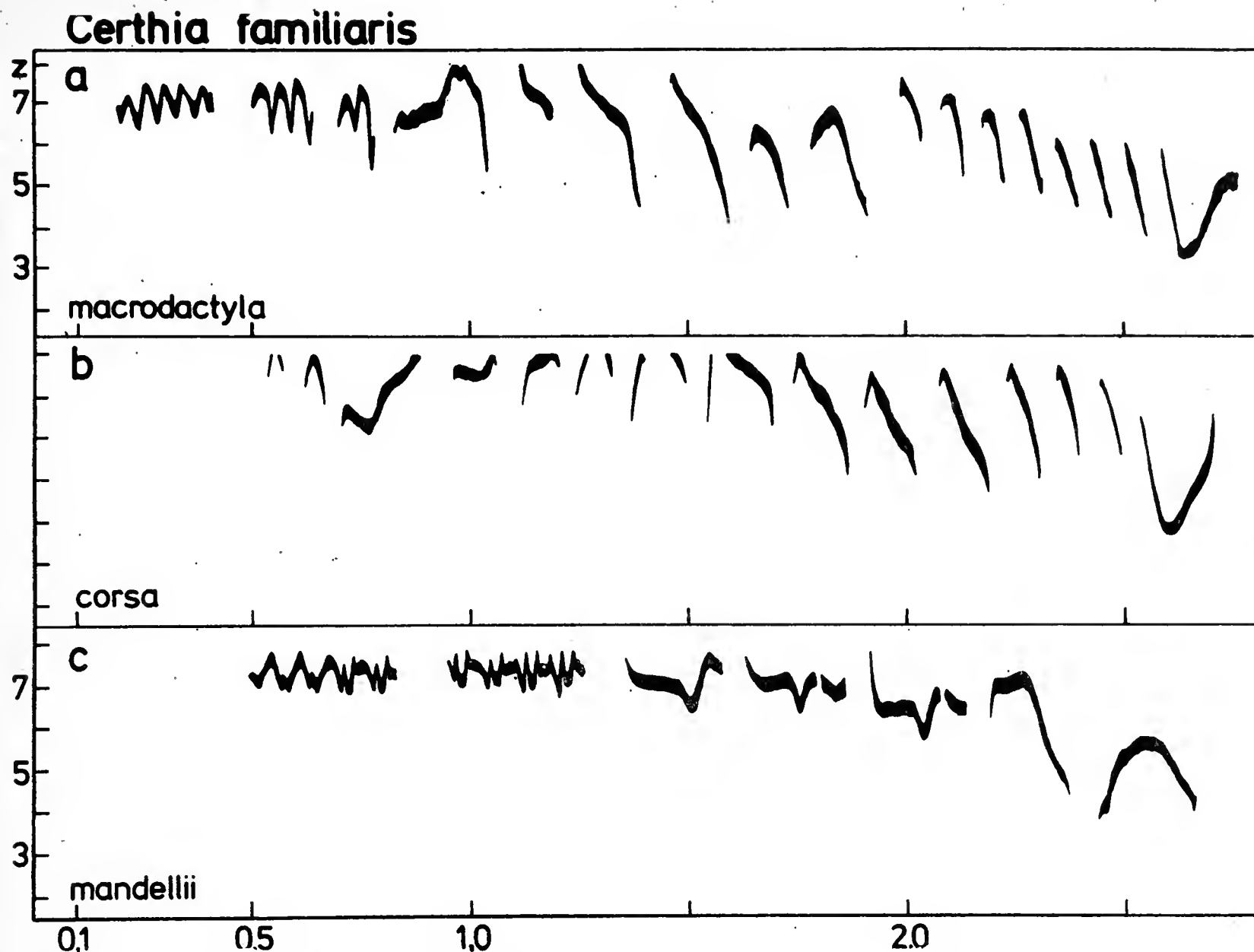


Fig. 8. Territorial songs of Certhia familiaris subspecies: macrodactyla (a, FRG, GDR), corsa (b, Corsica), mandellii (c, Nepal). Introductory elements in (a) and (c) differ in fine structure; they are used as calls for long distance contact (a, c) and rivalry (c). (c) — after Martens (1981)

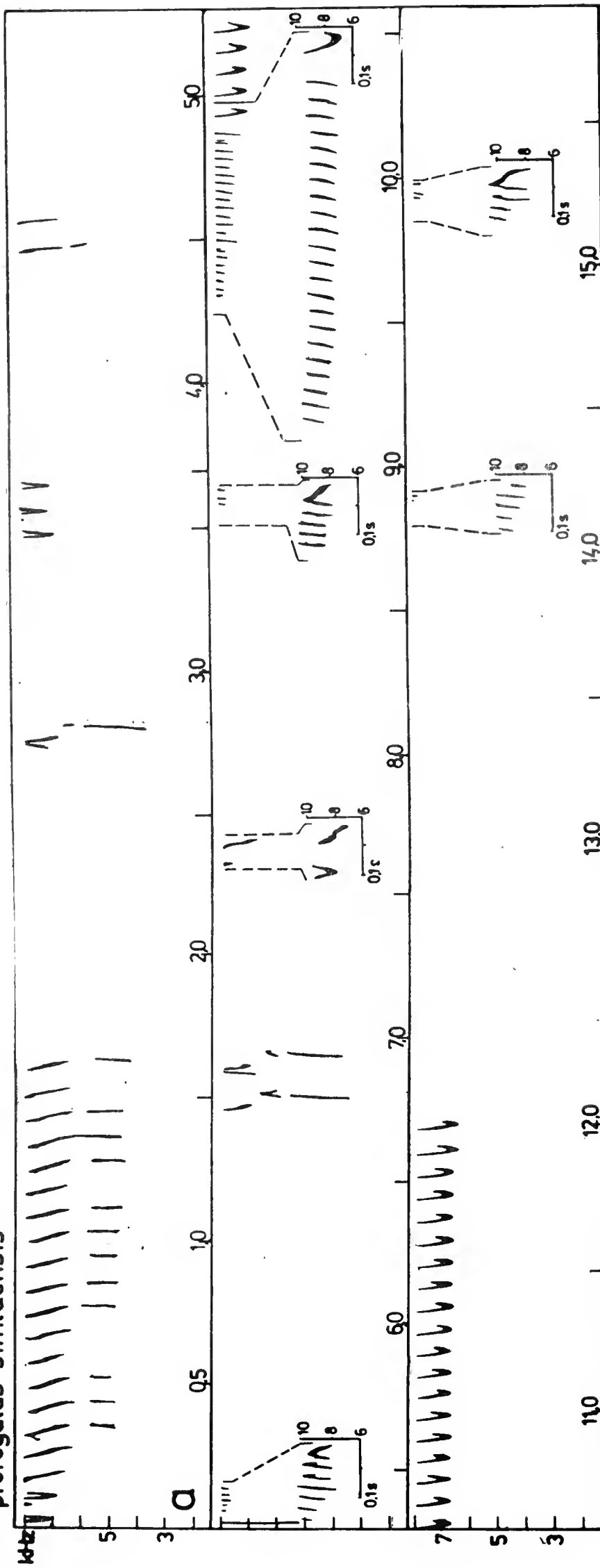
Phylloscopus proregulus

Distribution is in two largely disjunct areas in Siberia/Mongolia and the entire Himalayas and adjoining areas of South-West China. The subspecies in the Himalayas and China are: simlaensis and chloronotus from west to east. There is no doubt that from their morphology all the populations are conspecific. But the territorial songs point to ethological barriers between disjunct populations. The differences are (Fig. 9):

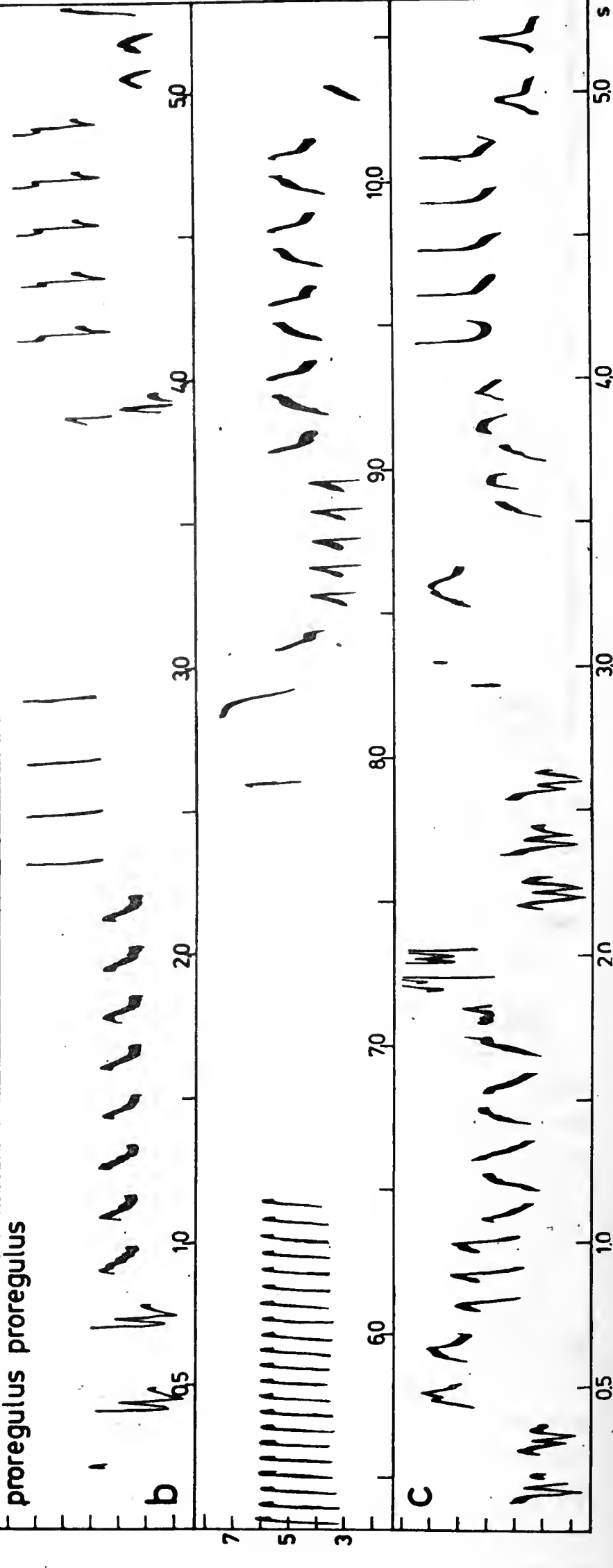
Himalayas-Lepal (simlaensis): song high pitched with many parts above 8 to nearly 12 kHz uttered continuously for several minutes. Within these long strophes we can distinguish repetition of one element once to several times, repetition of an element group (always two elements in a group), element groups divided into phrases (subdivision two to three times), and continuous change of the quality of an element within a group of three to seven elements. Frequency 4-11.5 kHz (Martens, 1980).

Siberia and Mongolia (proregulus): construction of the differently long strophes as repetitions of an element and as phrases of long element groups. The single element groups and phrases follow more closely to each other than in simlaensis and the repertoire of elements is richer. The frequency of the

proregulus simlaensis



proregulus proregulus



elements is lower, 1.5-8 kHz, the low songs prevailing, and the pitch of 7-8kHz is rarely reached.

Interpretation: The frequency range of p.proregulus song compared to p.simlaensis is lower by about 3 kHz. There is an even greater difference in the normal frequency which is difficult to explain. For physical reasons small birds usually use higher frequencies (Wallschlager, 1980). Siberian and Himalayan subspecies however are not different in weight so that frequency differences are difficult to understand. There are also differences in syntax and construction of the elements. All factors combined it seems very improbable that individuals from both areas would pair freely sympatric distribution presumed.

DISCUSSION

The endemic species of the Himalayas give little information how speciation processes influenced the development of the Himalayan avifauna. It seems preferable to look at closely related species or subspecies living outside the Himalayas. Regarding the geologically young age of the Himalayas it seems the greatest influence in speciation was in the Pleistocene glacial periods. At this time the Himalays proper probably did not act as a large scale isolated refuge for Palaearctic birds inspite of the huge mountain system (Martens, 1979). Hence the small number of endemics of less than 5% at the species level.

Even most of the few endemics did not develop there. Obviously the few remaining parts of the Palaearctic pine forests on the south slopes of the Himalayas were too small to house independent populations of most of the species in question during glacial periods. But we must remember that many Palaearctic species developed several well marked subspecies there (genera Phylloscopus, Certhia, Regulus, Parus, Tarsiger f.e.). They might have originated in small relic populations in the Himalayas and which met in post-glacial times when ecological conditions became more favourable. Regions with intensive speciation were however situated with certainty east and west in the close vicinity of the Himalayas. These areas were forested at times of intensive glaciation of the Northern Hemisphere. They acted not only as a refuge and evolution centres but also as points of dispersal in the post-Pleistocene. These were the Turkestan centre west of the Himalayas and the Yunnan centre to the east, the famous River Gorge Country. It was only after the last glaciation that the avifauna of Palaearctic and Indochinese affinities spread to the Himalays from the west and east forested countries. Closely related taxa can quite often be traced back to a common ancestor which sometimes, for varying periods, were separated in the western and eastern refuges. During this time they partly acquired mechanisms preventing hybridization and thus attained species status (see Table 1).

Fig. 9. Parts of territorial songs of Phylloscopus proregulus simlaensis (a, Nepal) and P.p.proregulus (b, Mongolia, Tereldsh)

Insets in (a) show elements above 8 kHz to different scales (a - after Martens, 1980, b - recorded by M.Schubert)

Many Himalayan birds with Palaearctic affinities occupy large areas in the Eurasian Taiga belt. In such cases another forest refuge influenced their recent distribution. This was in Mongolia or Manchuria near the Pacific coast. The Eurasian forest belt was settled from there after post-glacial times. Normally disjunct populations of the Himalayas and Taiga belt are only regarded as subspecies. This is shown in the slight morphological differences, but ethological investigations prove that in certain cases the populations in question might already have gained species status or nearly so (see Table 1).

SUMMARY

Well documented examples of the genera Phylloscopus, Parus and Certhia are given to demonstrate how speciation processes acted on the development of the Himalayan avifauna. It is shown that the Himalayas were not an important refuge for Palaearctic forest birds during Pleistocene but neighbouring areas to the west (Turkestan refuge) and to the east (Yunnan refuge). There new taxa evolved and spread into the Himalayas in post-Pleistocene time.

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HISTORICAL AND ECOLOGICAL EVIDENCE ON THE DEVELOPMENT OF MEDITERRANEAN AVIFAUNAS

Jacques Blondel

Centre d'Etudes Phytosociologiques et Ecologiques/CNRS:
route de Mende, B.P. 5051-34033, Montpellier, Cedex, France

INTRODUCTION

The palaearctic Mediterranean has a surface area of ca 2 970 000 km² and straddles three continents: Europe, south-eastern Asia and northern Africa. One of the main features of this territory is the extreme geotopographical and geobotanical diversity of habitats encircling or on the islands within this "sea-among-the-lands" (Mediterranean). For the biogeographer, islands, peninsulas and mountainous barriers are of utmost importance because of spatial isolation of taxa and discontinuity between habitats. This state of affairs explains the exceptionally high diversity of habitats from the arid steppes of northern Africa and the Middle-East to the moist fir-beech forests in the mountains of the continents and some large islands. This diversity has existed since the Pliocene, in spite of many geobotanical vicissitudes due to repeated glaciations, and has many repercussions on the richness of bird faunas. At the present time, we can find, only a few kilometers apart, but at different elevations, boreal elements such as the Tengmalm's owl (Aegolius funereus) and thermophilous mediterranean species such as the Sardinian Warbler (Sylvia melanocephala). This represents a striking telescoping of faunas which, as will be shown later, is a heritage of glacial times.

One of the most striking and puzzling facts which can be shown by studies of bird communities along ecological successions in the Mediterranean is that the more the vegetation comes near a mature climax state, the less the bird community looks "mediterranean" or, at least, of southern biogeographic origin (Blondel, 1979, 1981, 1983). Actually, in the old forests of holm oak (Quercus ilex) which together with the pubescent oak (Quercus pubescens) were proven to cover large areas in the Mediterranean area before their destruction by man, which started as far as 5 000 years ago, almost all bird species belong to boreal and temperate faunal types (sensu Voous, 1960), and the communities do not markedly differ from those of deciduous forests of Central Europe. We need to explain this paradox in the light of modern ecology and especially from the history of biotas in the Mediterranean.

ECOLOGICAL CHARACTERS AND BIOGEOGRAPHICAL ORIGIN OF MEDITERRANEAN BIRD FAUNAS

There are 335 species of breeding birds (various bibliographic sources)¹ in the 2 970 000 km² of the Mediterranean area; the number of species in the main continental subdivisions and on islands is shown in Fig.1. As could be predicted by current theories of island biogeography (Preston, 1962; Mac Arthur, Wilson, 1963, 1967), there is a strong correlation between species

¹ The list of species and their distributional area inside the Mediterranean basin can be obtained by writing to the author.

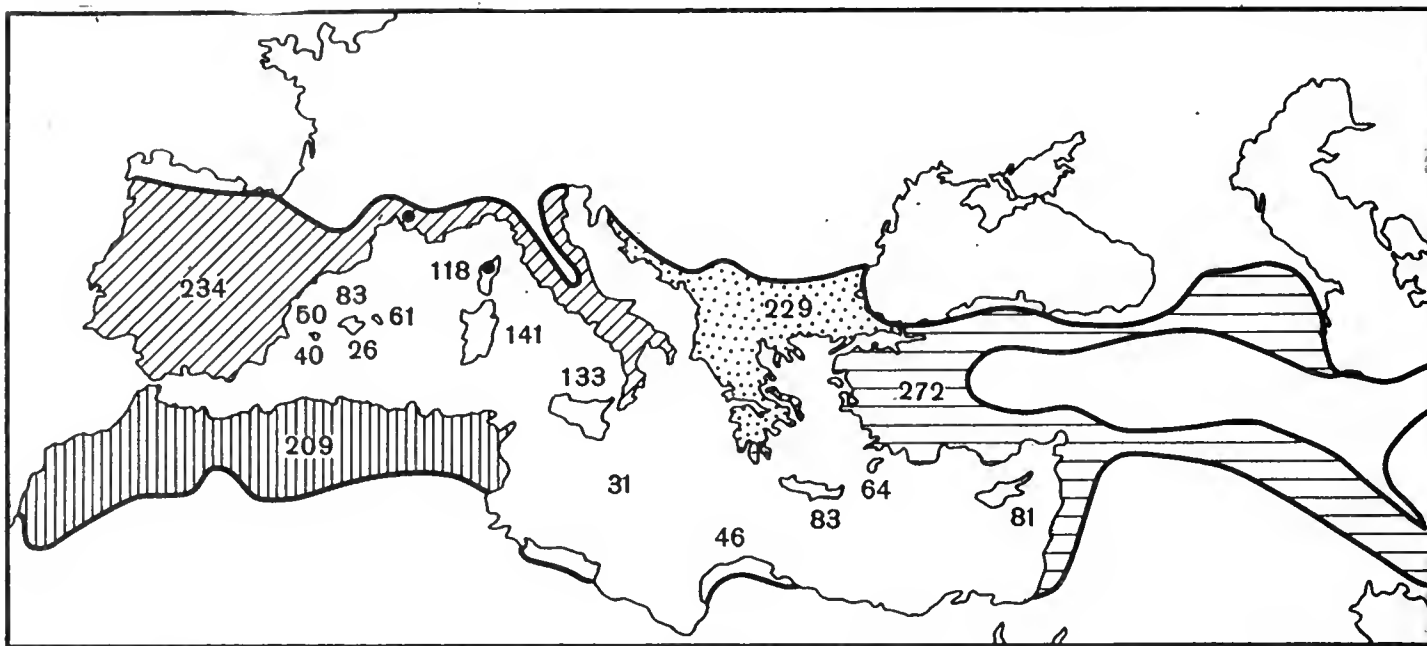


Fig. 1. Geographical limits of the Mediterranean area and the numbers of breeding bird species in mainland areas and 13 islands of the Mediterranean basin (Cyrenaica considered as a biological island)

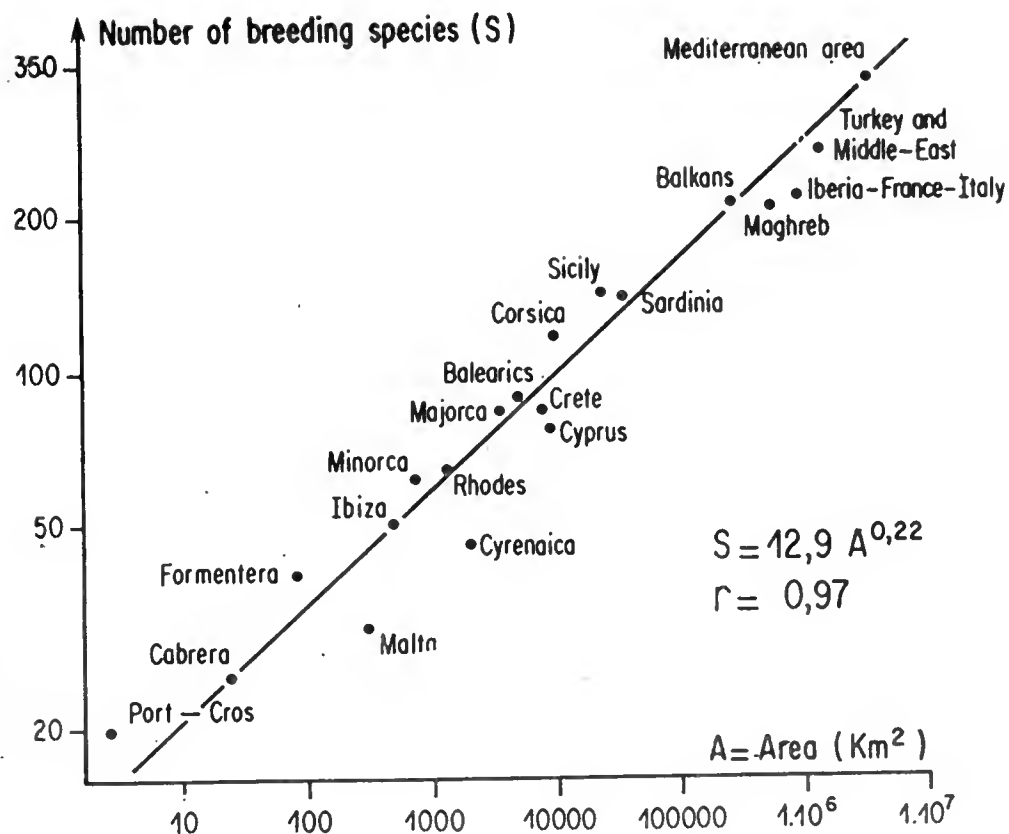
richness and area (Fig.2), which will not be discussed further here (see Blondel, 1979, 1982). This overall mediterranean richness must be compared with the 419 species breeding in the 10 100 000 km² of the whole of Europe (Voous, 1960). The ratio richness/area (S/A. 10⁻⁵) is therefore 4.15 for Europe but rises to 11.3 for the Mediterranean, and this must be related to the position of the Mediterranean facing three continents and to its physiographic diversity which increases species diversity. Moreover, topographical diversity and island effects promote geographical isolation, especially for sedentary species, which increases the probability of speciation at both specific (Sitta spp., Sylvia spp., Hippolais spp., Alectoris spp.) and infraspecific levels (cf. infra).

Ecological categories. The 335 species inhabiting the Mediterranean area can be classified into 5 main categories according to their broad habitat preferences. This classification is not intended to match certain earlier biogeographical classifications such as that of Voous (1960), but only to interpret the development of faunas in the light of the history of habitats.

Forest species. 74 species (22%) belong to this category. It is remarkable that these forest species (Picus, Picoides, Sitta, Turdus, Parus, etc.), which mainly belong to a boreal (holarctic or palaearctic) fauna, are regularly widespread everywhere even in the southern margin of the Mediterranean. The high proportion of forest species of boreal origin is an interesting phenomenon which must be interpreted in the light of the past history of the biotas. Several cues (paleontology, paleobotany, dynamics of bird communities along ecological successions) clearly suggest that sylvatic bird faunas in mediterranean forests are not different from those of the deciduous biome of Europe: no discontinuity, neither systematic nor biogeographic, allows one to detect any syndrome of mediterraneity.

Steppe species. With 92 species (27%), this category is actually the largest and comprises the great many species which evolved in the eastern and southern margins of the Mediterranean, which has been since the Tertiary a more or less broad belt of semi-arid habitats extending from the Atlantic Ocean to the steppes of Central Asia. Examples from this category are Geron-

Fig. 2. Relationship between the numbers of species and the superficy of the island and mainland areas



ticus eremita, Buteo rufinus, at least four vultures, Falco biarmicus, Falco cherrug, Falco naumanni, four Bustards, two Bee-eaters, and, among passerines, genera such as Calandrella, Chersophilus, Galerida, Oenanthe etc. The relative importance of this category has been strongly enhanced and brought northwards by the generalised withdrawal of forest vegetation due to human activity since the Neolithic, and many species in this category which were formerly rare and localised in the southern margins of the Mediterranean are widespread everywhere today. This category is of course especially well represented in the southern parts of the area: 31% of the avifauna in the Maghreb, 41% in Cyrenaica and in the very degraded islands of the eastern Mediterranean (28% in Crete, 38% in Rhodes and 32% in Cyprus).

Bush species. In the mind of most people, shrublike vegetation is likely to be typical of the Mediterranean, as is indicated by many terms to designate it: macchia, garrigue, matorral, chaparral, phrygana etc. Therefore, one would have expected this category to be dominant. Actually no more than 13% of the avifauna is adapted to and has evolved in a shrublike mediterranean vegetation with some typical genera such as Sylvia and Hippolais. Obviously, the palaearctic matorrals which are so widespread nowadays in the Mediterranean area have not been a theater for active speciation. The pollen analyses show a clear dominance of oak forests, especially of the broad-leaf Quercus pubescens, during post-glacial times and up to the beginning of human impact, some 4 000 years ago in the western Mediterranean and 6 000 years ago in the eastern (Triat-Laval, 1978; Pons, 1981). So, although some kinds of matorrals must have existed since the beginning of the Pleistocene (Suc, 1973) which have just allowed the adaptive radiation of the few truly mediterranean species, the generalised extension of shrubland is something new, obviously connected with human activity, as was demonstrated by palaeobotanists. Matorrals were probably too small and too patchy to allow the evolution of more than just a few species. The situation is very different with the entomofaunas and floras which undertook an active speciation: 50% of the 23 000 plant species of the region are of mediterranean origin (Quezel, 1981). But the proces-

ses of speciation for plants and insects can be achieved in small areas and in sympatric or stasipatric situations, which is unknown for birds (Mayr, 1963, 1970; Selander, 1965).

Rock species. These species adapted to rocks, cliffs and screes build up only a small fraction of the fauna, 7% to 14%. From a biogeographical point of view, it cannot be distinguished from the steppe fauna, and several of these species probably originated in the hot and dry mountains of the southern Palaearctic. Examples are Hieraaetus fasciatus, four Swifts, Columbia livia, three Swallows, the two Monticola, Pyrrhocorax pyrrhocorax.

Water birds. If we put aside marine birds (Procellariidae, Sulidae, Phalacrocoracidae, some Laridae) because their ecology and history are too different from those of land birds, two main subcategories must be recognised:

a) the birds of brackish mediterranean lagoons (3.3% of the fauna) which belong either to a fauna of holarctic or world-wide distribution (Haematopus, Himantopus, Recurvirostra, Tringa, Charadrius) or to a very old Messinian fauna which evolved in the ancient brackish sarmatic sea which extended during the Pliocene to the northeast of the modern Mediterranean sea. If not numerous, this fauna is very typical: Phoenicopterus ruber, Oxyura leucocephala, Anas angustirostris, Larus genei, Larus melanocephalus (Sarmatic faunal type of Voous, 1960).

b) the fresh-water birds which all belong to holarctic or palaearctic faunal types. This category is well represented in large continental areas (up to 21% of the whole fauna), but it is much more reduced on islands because of lack of fresh water: 26 species in Sardinia, 9 in Crete and only one in Malta.

BIOGEOGRAPHIC AFFINITIES OF THE MEDITERRANEAN BIRD FAUNA

Because of the geographic situation of the mediterranean area, it is interesting to look for the contribution of the adjacent land masses to the building of the modern bird fauna. In other words, what are the relationships between the mediterranean fauna and those of Palaearctic, Afrotropical and Oriental regions and what can be concluded about a truly autochthonous mediterranean bird fauna if any? In order to be more precise, about the biogeographic identity of a fauna, it is not sufficient to compare lists because the aim is to understand the present distributions in the light of the past dynamics of the faunas. Faunas are not homogeneous assemblages of species but a mixture and everchanging juxtaposition of taxa, the history of which must be analysed independently: "la répartition d'un complexe dépend d'une conjonction de circonstances dont la résultante est imprévisible" (Favarger, Kupfer, 1981). For this reason, any interpretation of the history of a fauna as a whole must be speculative and misleading. Nevertheless, some general trends can be seen from the present distribution of taxa.

RELATIONSHIPS BETWEEN MEDITERRANEAN AND AFRICA

Although many tropical groups such as Cracidae, Psittacidae, Musophagidae, Coliidae, Trogonidae and Bucerotidae among others were widespread in Eurasia during the Pliocene (Brodkorb, 1971), as well as the New World Vultures Cathartidae during the Oligocene, the relationships of modern avifaunas between the Mediterranean and Africa are rather scanty. The patterns of distribution of many families (Paridae, Sittidae, Prunellidae, Corvidae, etc.)

clearly show that their origin is holarctic. This means that, as early as the Tertiary, it must have been an efficient barrier (sea and/or desert) isolating avifaunas of Africa from those of Europe so that important evolutionary centres have been active somewhere in Eurasia. This is true also for floras since "tout cet ensemble méditerranéen est isolé du monde tropical par les vastes déserts qui ont dû apparaître à la charnière Miocène-Pliocène (Messinien)" (Favarger, Kupfer, 1981). This point being settled, what are the relationships between African and European avifaunas during the late Pleistocene, that is at a time when the species were about the same as now? Faunistic relationships are clearly much narrower between Eurasia and North America than between Eurasia and Africa, in spite of many contacts which must have taken place at tardi- and postglacial times. Snow (1978) has shown that, among the 419 breeding species of Europe (after Voous, 1960), 75 which are of palaeartic origin are also present in tropical Africa while only 6 species which breed in the Mediterranean area are of African origin and have conspecific populations in Africa: Falco biarmicus, Clamator glandarius, Ardeola ralloides, Fulica cristata, Cercotrichas galactotes, Cisticola juncidis. Three more species may be of afrotropical origin but this remains questionable: Upupa epops, Coracias garrulus and Merops apiaster. Contrary to what was sometimes claimed, tropical Africa got many more species from the north than it gave. Clearly, most of the species which breed in the Mediterranean area come from holarctic or palaeartic groups, an efficient barrier having acted against the penetration to the north of African species.

RELATIONSHIPS BETWEEN THE MEDITERRANEAN, ASIA AND AFRICA

In contrast, there are very close affinities between Mediterranean and Asiatic avifaunas, especially with the steppes of south-west Asia which many times in the past and up to now acts as a screen of "steppe Palaearctic" between the "forest Palaearctic" and tropical Asia. More than 100 species come from this part of Asia and strongly impregnate the bird faunas of the eastern part of the Mediterranean basin. Most of the genera now present in the Sahara belong to this fauna but progressively vanish to the south, where climatic conditions become more desertic. This fauna has become widespread in the open biotopes of the Mediterranean area and has benefited greatly from human deforestation. Most of the species that Mediterranean Europe, South-East Asia and North Africa share in common spread themselves over the three land masses at a time which is impossible to determine. The patterns of distribution were so modified by climatic vicissitudes of the Pleistocene, however, that it is not necessary to go back earlier than the last glacial period to interpret them. According to their patterns of distribution and taxonomic affinities, many species which are "Indo-African" according to Voous (1960) achieved their modern distribution thanks to the large Indo-African connection. Their exact origin is difficult to state and may be either in the steppic Palaearctic or in tropical Asia. These include, for instance, Ardea purpurea, Ardeola ibis, Neophron percnopterus, Aquila rapax, Hieraaëtus fasciatus, Circaetus gallicus, Accipiter badius, Turnix sylvatica, Porphyrio porphyrio, Elanus caeruleus, Glareola pratincola, Apus melba, Hirundo daurica as well as whole genera such as Pterocles, Alaemon, Oenanthe, Chersophilus etc.

SPECIATION IN THE MEDITERRANEAN AREA

It is very surprising to notice that out of the 335 species breeding in the Mediterranean area, very few evolved in mediterranean-type habitats like matorrals or chaparrals. This is in opposition with what happens for floras, since about 50% of the plant species are truly mediterranean (Quezel et al., 1981).

Some bird species evolved in forest habitats owing to geographical isolation; this is the case for the three endemic forest Nuthatches which belong to a superspecies: Sitta whiteheadi adapted to the Pinus laricio of Corsica, Sitta kruperi adapted to Pinus brutia and other conifers in Turkey, and Sitta ledanti the location of which is closely related to the small patches of the endemic Abies numidica in Algeria. Whereas the Corsican Nuthatch may be quite ancient because the isolation of the Corsican Sardinian block is as old as the Oligocene-Miocene the two other species may derive much more recently from an ancient form common to the three species, owing to fragmentation of forest habitats during the Pleistocene. Some other species strongly adapted to garrigues and macchias clearly evolved in this type of habitat inside or slightly to the south of the modern limits of the Mediterranean area. The best example is that of the Warblers of the genus Sylvia, which is truly palaearctic. There are 14 Sylvia species in the Mediterranean, and 10 of them are closely adapted to mediterranean-type vegetation. Their distributional area is exclusively Mediterranean and two are endemic on islands: Sylvia sarda in the western Mediterranean (Balearics, Corsica, Sardinia, Sicily and satellites islets) and Sylvia melanothorax (which forms probably a superspecies with S. melanocephala) in Cyprus. These species are quite similar and closely related, and it is probable that their radiation is no older than the late Pleistocene, evolutionary processes having taken place inside the modern boundaries of the Mediterranean owing to fragmentation and isolation during the glacial period, since we now know that a truly mediterranean vegetation was never absent in the region, even at the climax of the last glaciation (Pons, Quezel, 1981). Actually, pollen analysis shows that there were expansions and retractions of mediterranean vegetation with glaciations, and this was very favourable for speciation since this vegetation never disappeared (Pons in litt.). Many works in the last two decades have shown that the cyclic phases of expansion and retraction of habitats owing to climatic variations produced active speciation, for instance those of Mengel (1964) for Parulidae of Northern America, Haffer (1967, 1969, 1974) for Amazonian faunas, Moreau (1966b) for African birds, and Keast (1961) and Ford (1970) for Australian biotas. Some Turdids must be of Mediterranean origin: Diplootocus moussieri which is endemic in Northern Africa and the two Monticolas, Monticola solitarius and M. saxatilis, which are adapted to bare and rocky habitats. Another genus which has some typically Mediterranean species is Alectoris, with four allopatric but very closely related species: A. graeca, A. chukar, A. barbara and A. rufa. These species are a nice example of geographic replacement and they all are highly polytypic (Fig. 3).

Although many indices point out the importance of Pleistocene vicissitudes on speciation patterns for birds (see Selander, 1965 for American birds), it

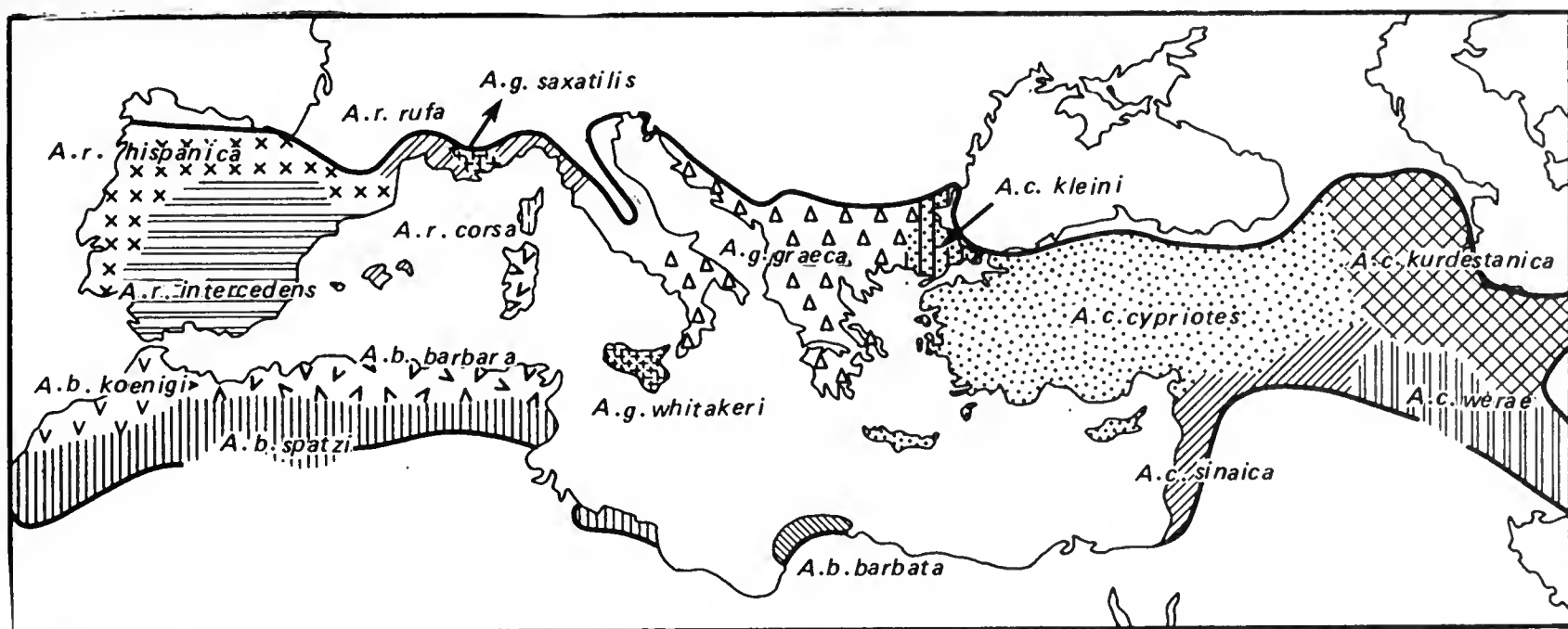


Fig. 3. Distributional map of the species and subspecies of Aleocharis in the Mediterranean basin

is very difficult to determine the chronology of the evolutionary processes in relation to these events because of their cyclic character, each glaciation having buffered or even obliterated the effects of the one before (Selander, 1971). This radiation can be quite recent, since we know that speciation can be achieved within some few thousand years (Moreau, 1966b: 376).

On the whole, among the 335 species now breeding in the Mediterranean area, only 44 (13%) are truly "mediterranean" and have evolved inside the Mediterranean biome in evergreen shrubland-type habitats. This is very few in regard to the great importance of boreal forest faunas and of steppe faunas which evolved in the southern and eastern margins of the Mediterranean area. Once more, we must point out that the situation is very different for plants (Favarger, Kupfer, 1981) and probably also for insects.

On the other hand there is a high variation at the infraspecific level, and most probably this variation is postglacial and related to the modern distribution of habitats just as they were progressively setting up after the last glaciation. On average, the 335 species of the Mediterranean area are represented by 5.4 subspecies per species at the scale of their worldwide distribution (after Vaurie, 1959, 1965), by 2.3 subspecies per species in the Palaearctic (Moreau, 1966a) and by 2.0 subspecies per species in the Mediterranean. But if these data are weighted by the inhabited areas in order to define an index of subspecific variation which gives an idea of the level of variability in the Mediterranean, in comparison with that of the whole distributional area of the species, this index is 0.56 for the Palaearctic region ($2.3/(41\,300\,000 \cdot 10^{-7})$) but rises to 6.73 for the Mediterranean ($2.0/(2\,970\,000 \cdot 10^{-7})$) ($2.0/(2\,970\,000 \cdot 10^{-7})$) (Table 1). This large difference must be related to the existence of isolates and the high evolutionary potentials of populations in the periphery of their distributional area, especially when topographic obstacles favour geographic isolation, which is the case in the Mediterranean.

Variation has been very high for land birds, especially passerines which are known to be more variable and to evolve more quickly than non passerines

T a b l e 1. Indices of subspecific variation of the birds breeding in the Mediterranean area: ISV – ratio of the number of subspecies per species the area ($A \cdot 10^{-7}$)

| Group of birds | Palaearctic | Mediterranean area | | |
|---|----------------------------------|--------------------|----------------------------------|------|
| | Number of subspecies per species | ISV | Number of subspecies per species | ISV |
| Water birds (N = 78) | 1.3 | 0.31 | 1.1 | 3.70 |
| Diurnal and nocturnal Raptors (N = 46) | 2.3 | 0.56 | 1.7 | 5.72 |
| Other non Passerines (N = 55) | 2.6 | 0.63 | 1.9 | 6.40 |
| Passerines (N = 153) | 2.7 | 0.65 | 2.6 | 8.75 |
| Total (N = 331) | 2.3 | 0.56 | 2.0 | 6.73 |

T a b l e 2. Number of subspecies per species for sedentary and migratory land birds on mainlands and on islands

| | N | Migratory | N | Sedentary |
|----------------|----|------------------|-----|------------------|
| | | Number of ssp/sp | | Number of ssp/sp |
| Mainland areas | 86 | 1.5 | 174 | 2.3 |
| Islands | 57 | 1.7 | 116 | 3.0 |

(Moreau, 1966a). This index of variation reaches its highest value for sedentary species on islands (Table 2), which is an indication of a high level of isolation of these populations.

THE ESTABLISHMENT OF MEDITERRANEAN AVIFAUNAS

From the above chapter it can be concluded that the Mediterranean bird faunas belong to three main faunal units: 1) boreal sylvatic, 2) southern and eastern steppic and semi-arid, 3) mediterranean, this last being very small. These units have evolved in quite different geographic areas and their occurrence in the region represents the inheritance of a long story closely linked with the bioclimatic vicissitudes of the late Pleistocene followed just afterwards by the impact of man, whose action has been drastic on Mediterranean landscapes for at least 4 000 years (Blondel, 1983).

Were the Mediterranean Bird Faunas Able to Survive Locally during the Quaternary?

Any attempt to interpret the history of modern bird communities must take into account the climatic events of the Pleistocene, especially the last which is the best known and the most important for our aim (see for instance Moreau, 1954). From a biogeographical and evolutionary point of view, what were the consequences of glacial times? First of all, it seems that almost all the ge-

nera and species known since the beginning of the Pleistocene are still alive in Europe (Lambrecht, 1933; Moreau, 1954; Mourer-Chauvire, 1975). This does not mean that glaciations have produced neither extinction nor speciation, but rather that, in spite of these huge climatic fluctuations, the major characters of the European avifaunas remained about the same. This idea, which is suggested by the study of fossil remains, is greatly enlightened by the examination of modern works on palaeobotany. These palaeobotanical studies show that at the maximum development of forest vegetation during the Atlantic period (7 500-4 500 BP), forests were widespread in many forms everywhere in the Mediterranean area (Pons, Quezel, 1981). But geographical isolates during the Pleistocene and the extreme palaeogeographical and palaeoclimatic complexity of the region together with the great orographic diversity and altitudinal zonation, which creates biological isolates, make especially difficult the reconstruction of the history of landscapes. What is most important is that contemporaneous floras were already present during the mid-Pleistocene and that climatic fluctuations have modified their local distributions rather than their composition (Bazille-Robert, 1979). Thus, the biological consequences of the diversity of habitats described by the botanists are quite important: the persistence of a mosaic of habitats, even at the most severe phase of the last glaciation (Reille, 1975; Triat-Laval, 1978; Bazille-Robert, 1979; Pons, Quezel, 1981) suggests (if it was the same for earlier glaciations) that during the whole Pleistocene, even during the coldest phases, the conditions have remained for the survival at least locally of all the species, including the most thermophilous. The unquestionable presence of the Hermann Turtle Testudo Hermanni at Würm II in Provence is a good indication for this (Cheylan, 1981). Anyway, the local survival of Mediterranean plant taxa during the last glaciation is now well established and allows us to explain the very fast expansion of the Mediterranean vegetation during the interglacial times (Vernet, 1972, 1979; Favarger, Kupfer, 1981). This means that the climatic conditions were probably less severe than formerly believed, at least locally. Some general trends in the development of Mediterranean avifaunas can be guessed in the light of palaeoecology and with reference to the biology of modern birds, making the assumption that ecophysiology and behaviour of the species were about the same as they are now, which seems reasonable (Selander, 1965).

Fossil Remains

What can we learnt from the fossil data? Although Pleistocene faunas do not look very different from modern ones (Brodkorb, 1971), the contribution of fossils is unfortunately limited for several reasons, the first of all being the poor fossilisation of a pneumatic skeleton and the difficulty to assess specific characters for determination of many species, especially passerines: "A large but uncertain proportion of existing species would not be separable on skeletal characters, especially given such imperfect material as usually has to serve the avian palaeontologist... if every species that had been alive at a given date in the past had left fossil remains, the most meticulous worker could never have diagnosed more than some fraction of them at the specific level" (Moreau, 1966: 406). Another difficulty is that the number, nature and amplitude of the climatic fluctuations during

the Pleistocene are such that the fossil remains must be located with great precision in the chronostratigraphic layers or be dated in absolute values (^{14}C), which is very difficult and has barely been done, with the exception of some modern works (e.g., Mourer-Chauvire, 1975). Moreover, the mobility and migratory habits of many species make uncertain their belonging to some "local fauna" described by palaeontologists who, too often, give only lists without biological considerations. How, then, can one know if a bird found in a deposit is not a transient introduced only by chance? Therefore, only sedentary species should be taken into account to reconstruct the history of a local fauna, even though it is quite possible that migratory habits have been modified according to climatic oscillations. Finally, fossil data are always characterized by an overrepresentation of non-passerines, especially of large species: water birds (the probability of fossilisation is better than for land birds), raptors and Galliformes. Thus, 48% of the Pleistocene fossil species are water birds and only 16% are passerines, whereas the modern faunas show only 11% of the former and 59% of the latter (Moreau, 1966a). Yet from an ecological point of view, passerines are the best ecological indicators for habitats and general conditions of life at a given time. Actually, the composition of fossil remains is particularly puzzling: many lists are heterogeneous assemblages of species obviously adapted to quite different habitats and bioclimates. For instance, Mourer-Chauvire (1975) found in two deposits of Würm II (Grotte du Prince, Monaco) such different types of species as several Anas, Gyps fulvus, Accipiter gentilis, Haliaetus albicilla, Lagopus mutus, Lyrurus tetrix, Alectoris sp., Vanellus vanellus, Gallinago media, Pyrrhocorax pyrrhocorax etc. As for the birds she found in l'"abîme de la Fage, Corrèze, France" which pertain to the Riss glaciation, their eclecticism is disconcerting: how to interpret such lists where one finds side by side Oceanodroma leucorhoa (pelagic bird of the Northern Atlantic), Falco naumanni (thermophilous mediterranean raptor), Lagopus mutus (bird of the tundra or of the alpine belt), Nyctea scandiaca (arctic owl), Monticola saxatilis (oromediterranean saxicolous Turdid) etc. Such puzzling and apparently aberrant assemblages necessarily lead to the following alternative: either the contemporaneity of these birds is doubtful and these mixtures correspond to separate times or they reflect at a local or regional scale a close juxtaposition of such different habitats as tundras with Nyctea scandiaca, forests with Garrulus glandarius and steppes with Falco naumanni. If this last explanation is right, and many indications make it plausible, it would signify an extraordinary telescoping of the European faunas, which would have concentrated themselves in the southern parts of Europe, taking advantage of this kaleidoscope of habitats created by the physiographic diversity of the Mediterranean basin. After all, why not assume that what seems unbelievable in the interglacial time where we live, that is the juxtaposition in a much smaller area than today of both "cold" and "warm" faunas, of forest and tundra faunas, did not happen during the glacial times? If such was the case, this hypothesis would unveil the disconcerting aspect of the fossil deposits and would not be contradictory with the plausible history of the bird faunas since the beginning of glacial times. In any case, whatever the difficulties to date these faunas, their specific composition strongly suggests that the Me-

diterranean regions of southern Europe and northern Africa have been able to maintain all the faunal types of Europe and this even at the height of the glaciations. Hence a remarkable resilience of bird faunas of different origin through the climatic vicissitudes. As a matter of fact, Robert-Bazille (1979) noticed that "la dynamique de la végétation se traduit par une alternance spatio-temporelle de pluviaux boisés et d'interpluviaux steppiques sans que ces deux types de végétation ne soient jamais exclus de la région". This is relevant to the hypothesis of the survival and coexistence of all the faunal types of the Palaearctic in the Mediterranean, since many types of vegetation, both deciduous and evergreen, wooded and steppic boreal and mediterranean, have been present side by side like a mosaic in this topographically diversified region.

The Mediterranean Basin as a Refuge for the European Bird Faunas During the Glacial Times

As already shown, more than a quarter of the species of the European bird faunas are sylvatic and have evolved in the Palaearctic and Nearctic regions, the contribution of tropical faunas having always been very small since the beginning of the Pleistocene, which strongly contrasts with what happened in North America where many families (i.e. Tyrannidae, Vireonidae, Icteridae, etc.) are of neotropical origin (see Mayr, 1946). This necessarily means that during the most severe phases of the glaciations, these faunas must have been driven down into the only wooded refugia which could have persisted on more or less large areas, namely the three peninsulas (Iberian, Ligurian and Balkan), the large Mediterranean islands, the surface of which was larger than now because of the general lowering of the sea level (Bonifay, 1962), and northern Africa up to the margins of the Sahara, which was at these times less wide and dry than now although never absent as a desert. It is in these regions that the forest faunas which make up the background of the European faunas (Turdus, Parus, Sitta, Picus, Picoides, Certhia, Prunella etc.) did survive. But these forests were rather fragmented, isolated and encircled by steppes, a situation particularly propitious for speciation, at least at the infraspecific level. Such a situation explains the high index of variability of land birds in the Mediterranean, especially for sedentary ones as is shown at both specific (Fig. 3 for Alectoris genus) and intraspecific (Fig. 4 for Garrulus glandarius) levels. Even if it is not possible to know when this geographical variation took place, geographical and ecological isolates created by repeated climatic fluctuations could but increase it. And since patches of truly Mediterranean vegetation (Oley, Quercus, Pinus, Mediterranean Abies) did survive locally, it is to be expected that they insured the survival, and perhaps the speciation, of the few truly Mediterranean species such as Sylvia spp. and Hippolais spp. In this respect, it is significant that Bate (1928) has found in Mousterian deposits near Gibraltar such Mediterranean species as Hieraaetus fasciatus and Falco eleonora among thirty or so forest species. Beug (1967, 1975) described the succession of postglacial vegetation types on the Dalmatian coast and has shown that a forest vegetation dominated by Quercus pubescens was dominant until 8400-7500 BP. The Mediterranean Quercus ilex appeared later (6500 BP) in pollen diagrams and achieved a climax only since 6300 BP, probably as a result of

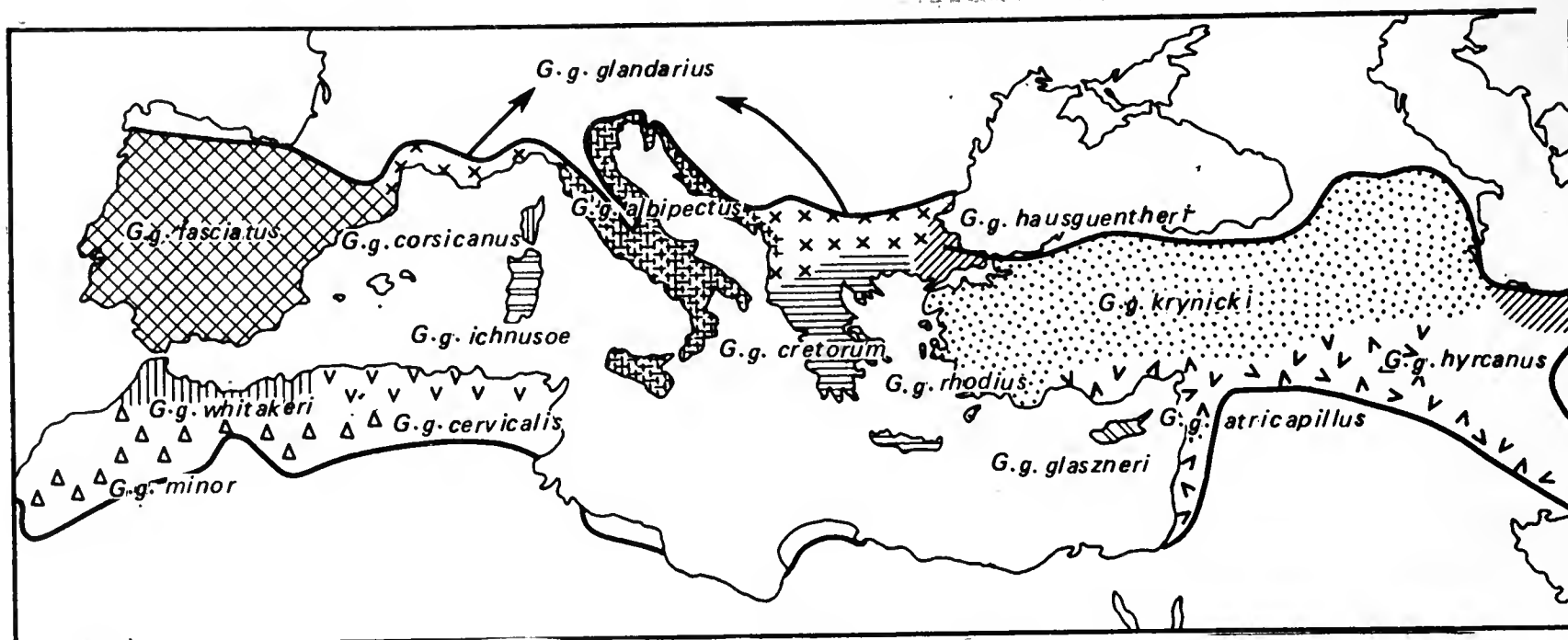


Fig. 4. Example of a highly polytypic species within the Mediterranean area: the sedentary Jay Garrulus glandarius (see text)

the impact of man. This was fully confirmed in the French valley of the Rhône river by Triat-Laval (1978) and by Pons and Quezel (1981). About 8 500 BP most of the lowland forests, at least in the European part of the Mediterranean basin, were still of submediterranean type with Quercus pubescens as a dominant tree, and it was not before the postglacial climatic optimum (Atlantic, 7 500 BP) that a typical Mediterranean forest dominated by Quercus ilex was spreading. Obviously, the faunas of these forests were temperate European and had nothing to do with the kind of fauna we think of when we speak of mediterranean vegetation as it looks now. As a matter of fact, it is now clear that the increasing "mediterraneity" of the faunas of the Mediterranean basin is nothing more than the result of the degradation of forests by man (see Blondel, 1983).

At the height of the last glaciation, virtually no forest species could find a suitable habitat to the north of the Pyrénées and the southern foot of the Alps and the Carpathians: the whole forest-bird fauna of Europe must have withdrawn to the Mediterranean refuge and only in them, since Favarcet, Kupfer (1981) have shown that although less severe than today, the Sahara could not have been suitable for temperate biotas.

To sum up, it seems as if the present situation, which is interglacial, has allowed the northward expansion of a fauna which in other times could only survive in the geographical limits of the Mediterranean, and this holds true also for the floras (Pons in litt.). In such a situation, it is not surprising that the birds of this region, especially forest birds and freshwater birds which make up altogether more than half of the species in Mediterranean Europe and northern Africa, do not show any syndrome of "mediterraneity". Only a very tiny proportion of the fauna is native in the shrublike vegetation which covers at the present time the greatest part of the region but which is a secondary vegetation.

SUMMARY

335 species of birds breed in the 2970000 km² of the Mediterranean basin. These species are classified into four main ecological categories which are discussed: forest species, bush species, rock species and water birds. The great bulk of the species are originating either from the forested Palaearctic or from the steppic habitats of the eastern and southern margins of the Mediterranean but very few evolved inside the bioclimatic limits of the Mediterranean area. Some examples are the Nuthatches in the conifer forests and the warblers of the genus Sylvia in shrublike habitats. On the other hand, there is a high infraspecific variation due to geotopographical diversity which creates biological isolates. Paleontological and paleobotanical cues show that most of the European forest species did survive in the Mediterranean during the glacial times and that the present interglacial situation is characterized by a shifting toward the north of faunas which otherwise would be at home in the Mediterranean. Thus except for a very small fraction of the avifauna (no more than 13%) it is difficult to speak of a "Mediterranean bird fauna". As a matter of fact the more the vegetation is near a climactic state (forest), the less the bird community looks "Mediterranean". It is clear that the increasing "Mediterraneity" of the bird faunas since some thousands years is nothing more than the result of the degradation of forests by man which lasts since at least 4000 years.

ACKNOWLEDGEMENTS

This work was partly financed by grants of the CNRS (Greco "Forêt méditerranéenne"). I am indebted to A. Pons who criticized a first draft of the manuscript and to E. Box who improved the English.

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SYMPOSIUM

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ENERGETIC COSTS AND ENERGY-SAVING MECHANISMS IN PARENTAL CARE OF FREE-LIVING PASSERINE BIRDS AS DETERMINED BY THE $D_2^{18}O$ METHOD

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BASAL METABOLIC RATE, THERMOREGULATION AND EXISTENCE ENERGY IN BIRDS: WORLD DATA

SIMULTANEOUS ESTIMATES OF DAILY ENERGY EXPENDITURE USING TIME-BUDGET ANALYSIS AND DOUBLY LABELED WATER

Wesley W. Weathers, Kenneth A. Nagy, William A. Buttemer
Department of Avian Sciences, University of California, Davis,
CA 95616 and Laboratory of Biomedical and Environmental Sciences,
UCLA, Los Angeles, CA 90024, USA

The belief that many fitness-related questions can be answered by understanding how birds expend time and energy has inspired numerous time-budget analyses of total daily energy expenditure (\dot{H}_{TD}) (reviews by King, 1974; Mugaas, King, 1981). Although these analyses provide insight into daily activity patterns, the accuracy of their \dot{H}_{TD} estimates is uncertain. This paper (presented here in extended abstract form) examines the reliability of time-budget and doubly labeled water estimates of \dot{H}_{TD} .

DOUBLY LABELED WATER (DLW) METHOD

This method employs isotopically labeled water ($^3\text{HH}^{18}\text{O}$ or $^2\text{HH}^{18}\text{O}$) to measure CO_2 production (for review see Nagy, 1980). Validation studies on endothermic species (Hails, 1979; Nagy, 1980) demonstrate that the DLW method measures CO_2 production with a mean error of +1.2% (range: -4 to +5%). Under some conditions (e.g., in fossorial species) errors can be much larger, and this can limit the method's reliability (see Nagy, 1980). Because the thermal equivalent of CO_2 varies by up to 23%, depending on the nature of the metabolized substrate, converting CO_2 production to energy expenditure requires knowledge of the animal's diet. Due to uncertainty about the diet of free-living birds, and technical errors in the labeled water analysis, \dot{H}_{TD} estimates based on the DLW method may contain errors of up to 10%.

TIME-ACTIVITY-LABORATORY (TAL) METHOD

This method quantifies field behavior through time-budget analysis and assigns energy costs to the different behaviors based on laboratory measurements or, more commonly, on speculative reasoning (see Mugaas, King, 1981). In theory, the TAL method can estimate \dot{H}_{TD} reasonably accurately if (1) the time budget is accurately known, (2) measured energy equivalents are assigned to behaviors, and (3) the thermal conditions surrounding the bird are known. Lack of information regarding a behavior's thermal consequences in complex natural environments raises doubts about this method's reliability in gauging \dot{H}_{TD} .

Utter (1971) used TAL and DLW methods simultaneously to estimate \dot{H}_{TD} of mockingbirds (Mimus polyglottos). Although the two methods produced comparable \dot{H}_{TD} estimates (mean difference 17%), this was undoubtedly fortuitous as Utter's TAL method did not account for the thermal environment's effect on \dot{H}_{TD} . In Phainopepla nitens, a TAL model that partially accounted for thermal effects produced \dot{H}_{TD} estimates that averaged 40% lower than simultaneous DLW estimates (Weathers, Nagy, 1980). The error analysis indicated that the Phainopepla TAL model fell short because it did not adequately characterize the bird's thermal environment.

To further assess this discrepancy, we simultaneously estimated \dot{H}_{TD} of captive Budgerygahs (Melopsittacus undulatus) during winter (January and February) with $^3\text{HH}^{18}\text{O}$ and a TAL model that combined careful assessment of the bird's thermal environment with accurate time-activity budgets and laboratory measurements of activity costs. This paper presents our preliminary results.

In brief, our protocol was as follows. An individual bird was injected with DLW and released in a large outdoor aviary (12m x 6m x 4m). Aviary wind and temperature profiles, as well as radiational fluxes and intensities, were monitored at 10 min intervals throughout the following 24 h. Estimates of operative temperature (T_e) were obtained using unheated taxidermic mounts (Bakken et al., 1981). Behavioral observations throughout the bird's diurnal active phase were encoded continuously with a microprocessor.

We used the time-activity and T_e data to estimate the Budgerygah's \dot{H}_{TD} (kJ/day) by this equation:

$$\dot{H}_{TD} = [t_{\alpha}(\dot{H}_{b\alpha} + TR_{\alpha})] + [t_{\rho}(\dot{H}_{b\rho} + TR_{\rho})] + [\dot{H}_F t_F + \dot{H}_{AP} t_{AP} + \dot{H}_G t_G + \dot{H}_E t_E + \dot{H}_M t_M].$$

The first two sets of bracketed terms concern basal and thermoregulatory requirements, where t_{α} and t_{ρ} represent the duration of diurnal and nocturnal phases, respectively. $\dot{H}_{b\rho}$ = the minimal or basal energy requirement during the rest phase (ρ) of the daily cycle, $\dot{H}_{b\alpha}$ = the minimal energy requirement during the day (α), and TR = the thermoregulatory requirement when T_e was below the bird's lower critical temperature. The third set of bracketed terms concerns the energy cost of activity, where \dot{H} is the rate of energy expenditure (kJ/h), and t is the number of hours per day spent in flight (F), alert perching (AP), grooming (G), eating (E), and miscellaneous activity (M). Miscellaneous activity, which consisted largely of lateral (shuffling) movements as birds changed perches, averaged 0.67 h/day.

To make our TAL estimates more accurate, we measured each bird's basal, thermoregulatory, and activity costs in the laboratory. We determined the basal and thermoregulatory requirement by measuring fasting oxygen consumption ($\dot{V}\text{O}_2$) at various T_e s during the rest phase (for methods see Weathers et al., 1980). The active phase metabolic requirement was estimated as 1.3 times the rest value (Weathers, Schoenbaechler, 1976). Using fed birds within their thermoneutral zone, we measured the various behaviors' energy costs—except for flight, which requires 29.2 kJ/h (Tucker, 1966). The measured behavior cost includes not only the activity's energy cost but the basal requirement, productive costs (if any), and the heat increment of, feeding during the measurement period. Subtracting $\dot{H}_{b\alpha}$ from the measured behavior costs yielded the following "activity" costs: alert perching 0.75 kJ/h, grooming 0.98 kJ/h, eating 1.12 kJ/h, and miscellaneous activity 1.03 kJ/h. We used each bird's actual activity cost, rather than the pooled mean, in our TAL calculations.

COMPARISON OF TAL AND DLW RESULTS

Despite accounting explicitly for all of the TAL model's component costs, our TAL estimates of \dot{H}_{TD} averaged 18% lower than DLW estimates (Table 1). This may reflect the limitation of using T_e alone to characterize the bird's thermal environment. For endotherms, T_e does not fully account for convective heat exchange (Bakken, 1980; Bakken et al., 1981). A plot of the difference

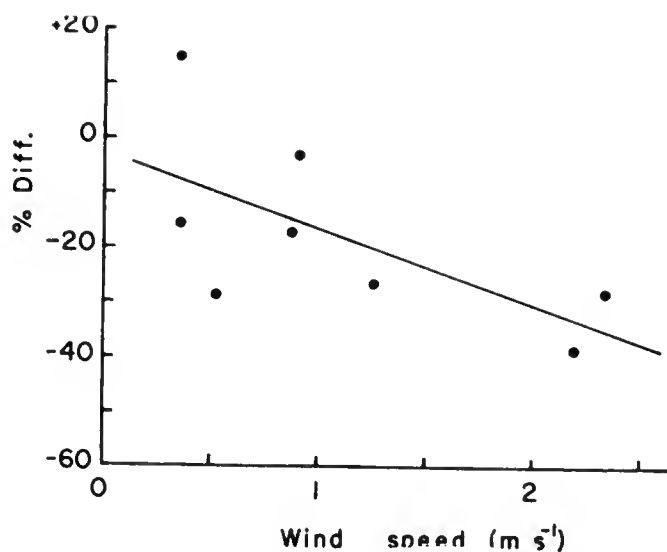


Fig. 1. Relation of the difference between doubly labeled water and TAL estimates of Budgerygah daily energy expenditure to mean daytime wind speed measured 2 m above ground. The line, fitted by least squares, is described by the relation $\% \text{ Diff.} = 3.0 - 13.6 \text{ m} \cdot \text{s}^{-1} \text{ (} r = 0.626 \text{)}$

Table 1. Comparison of doubly labeled water ($^3\text{HH}^{18}\text{O}$) and time-activity-laboratory (TAL) estimates of Budgerygah daily energy expenditure (\dot{H}_{TD})

| Animal N | Mass (g) | \dot{H}_{TD} (kJ/day) | | % Diff.* |
|---------------|----------------|--------------------------------|----------------|------------------|
| | | $^3\text{HH}^{18}\text{O}$ | TAL | |
| 78 | 29.5 | 89.5 | 74.4 | -16.9 |
| 295 | 32.7 | 104.0 | 76.4 | -26.6 |
| 26 | 33.4 | 77.9 | 89.5 | +14.9 |
| 91 | 33.5 | 123.3 | 76.3 | -38.1 |
| 78 | 29.5 | 109.3 | 78.8 | -27.9 |
| 786 | 33.8 | 108.9 | 77.0 | -29.3 |
| 102 | 32.1 | 94.5 | 79.3 | -16.1 |
| 295 | 32.9 | 76.6 | 74.3 | -3.0 |
| Mean \pm SD | 32.2 \pm 1.7 | 98.0 \pm 16.3 | 78.3 \pm 4.9 | -17.9 \pm 17.0 |

* % Diff. = $100 (\text{TAL} - ^3\text{HH}^{18}\text{O}) / ^3\text{HH}^{18}\text{O}$

between DLW and TAL estimates versus mean daytime wind speed (measured at 2m) indicates that the TAL method progressively underestimates \dot{H}_{TD} as wind speed increases (Fig.1). (Birds used protected roost boxes at night.) The least squares regression line indicates little difference between the two estimates at zero wind speed. Although this may be fortuitous, it implies that the TAL method would benefit from the inclusion of convective heat transfer components.

SOURCES OF ERROR IN TAL ESTIMATES

Because flight is metabolically expensive (typically $12 \times H_b$), errors in its cost estimate are often thought to contribute most to errors in the \dot{H}_{TD} estimate. But, except for aerial insectivores, migrants, or adults feeding nestlings, most birds spend relatively little time in flight, often less than 10% of a 24-h day. Consequently, flight typically accounts for less than 25% of \dot{H}_{TD} . Errors in a component's cost estimate produce errors in the TAL estimate of \dot{H}_{TD} that are directly proportional to the component's fractional contribution to \dot{H}_{TD} (i.e., error in \dot{H}_{TD} = component's fraction of \dot{H}_{TD} \times % error in component's assigned cost). Hence if flight costs account for 25% of \dot{H}_{TD} , and the \dot{H}_F estimate is 25% too high, the \dot{H}_{TD} estimate will be 6.25% too high ($0.25 \times 25\%$). Clearly, those components that contribute

most to \dot{H}_{TD} present the greatest potential sources of error. Because basal and thermoregulatory requirements often represent 40 to 80% of \dot{H}_{TD} (Ettinger, King, 1980), errors in estimating their costs may contribute most to errors in the TAL estimate of \dot{H}_{TD} . Our Budgerygah data confirm this by suggesting that better estimates of the thermoregulatory requirement (by including convective heat transfer) would have led to better TAL estimates.

SUMMARY AND RECOMMENDATIONS

TAL models can accurately estimate \dot{H}_{TD} , provided all of the conditions specified above are met. In this study, T_e appeared to be an inadequate measure of the thermal environment. T_{es} , which accounts for convective heat transfer in endotherms, should be a more appropriate index of heat exchange in birds. TAL models less robust than the one we used are unlikely to produce reliable results. For example, when we estimated the Budgerygah's \dot{H}_{TD} using Utter's (1971) method, the result (33.4 kJ/day) was 65% lower than the DLW estimate.

The doubly labeled water and TAL methods are complementary, not competing, techniques. The TAL method furnishes information not provided by the DLW method; namely, how birds pattern their activity, whereas the DLW method provides relatively accurate estimates of daily energy expenditure. Using both techniques simultaneously is the best way to gain insight into how birds allocate time and energy.

ACKNOWLEDGMENTS

Support provided by National Science Foundation grants PCM76-18314 and DEB80-22765, and U S Department of Energy Contract DE-AM03-76-SF00012. We thank Anita M. Hayworth for her technical assistance.

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ENERGETIC COSTS AND ENERGY-SAVING MECHANISMS IN PARENTAL CARE
OF FREE-LIVING PASSERINE BIRDS AS DETERMINED BY THE $D_2^{18}O$ METHOD¹

Klass Westerterp², Rudolf Drent

University of Limburg, Department of Human Biology,
6200 MD Maastricht, The Netherlands;

Zoological Laboratory, University of Groningen, Haren (Gr), The Netherlands

The crucial resource in the life of a bird may often be energy. Studies so far have to rely heavily on extrapolation from captive conditions in order to delimit the energy needs for reproduction (King, 1974; Ricklefs, 1974). Little is known about the energy costs of free existence, and rarely is it possible to evaluate the energetic consequences of alternative types of parental behaviour. Development of the doubly-labeled water technique (Lifson, McClintock, 1966, for a recent review see Nagy, 1980) allows observation on free-ranging birds. Using this method we measured energy expenditure and simultaneously observed the activity of the subject: breeding birds. We report data on seven species: Sand Martin (Riparia riparia), Swallow (Hirundo rustica), House Martin (Delichon urbica), Blue Tit (Parus caeruleus), Great Tit (Parus major), Starling (Sturnus vulgaris) and Pied King Fisher (Ceryle rudis).

The Starling was most suitable for full time behavioural observations. Here we could calculate the costs of the main types of behaviour: sitting, foraging and flying. The energy expenditure of the most costly of these three, flying was measured in greater detail in relation to flight speed by field experiments in which flight distance was manipulated. Finally we present evidence that flight costs during the breeding season are minimized by reduction of body mass.

METHODS

Birds were captured for the introduction of labeled water, blood sampling, making and weighing (Bryant, Westerterp, 1980). Usually they were caught at dusk, close to or on the nest, and either released to fly to the roost or replaced in the nest when appropriate. Daytime activity was recorded at the nest in all species.

Starlings were observed in two breeding colonies in the Netherlands: Vosbergen, a mixed woodland with dispersed feeding grounds at least 100 m away from the breeding site; and Schiermonnikoog, a grassland and salt marsh area with feeding grounds next to the breeding site. On Schiermonnikoog were no big trees or other obstacles. Here, full daytime coverage of the birds' behaviour at the nest as well as in the field could be reached from a high observation point.

In the Starling we measured costs of flight, foraging and sitting in three types of observations:

¹ Results from a joint project with the Institute for Ecological Research, Arnhem and the Max-Planck-Institut für Verhaltensphysiologie, Seewiesen.

² Supported by the Netherlands Foundation for the Advancement of Pure Research (ZWO).

1. Simultaneous energy time-budget of breeding birds, measuring ADMR (average daily metabolic rate) and overnight metabolic rate, observing the birds in daytime and calculating the costs of the three types of behaviour with regression analysis.

2. Measuring flight costs of long distance flight by displacing birds 10-30 km from their nestbox.

3. Simultaneous time and energy-budgets of birds foraging in a 1 x 7 m cage on the feedings grounds, making only short flights.

Body mass changes of Starlings were recorded in early spring, before laying, and during incubation and nestling feeding. In early spring the birds were caught at night while roosting in the nestbox and weighed with a spring balance. Breeding birds were weighed without trapping, with an analytic balance under the nest (Westerterp et al., 1982). Body mass changes were further analysed and split into changes of fat content and lean dry mass as determined by soxhlet extraction in a sample of 15 carcasses. Energy expenditure, as measured with the doubly-labeled water technique in ml CO₂ was converted to Joules with an equivalent depending on the food consumed and the consequent RQ (ranging from 0.75 to 0.85). To compare between individuals and species, metabolic rate (MR) was corrected for body mass differences by expressing MR as a multiple of BMR (basal metabolic rate) using the equation for the inactive phase (night) of Aschoff and Pohl (1970):

$$\text{BMR} = 5.55 M^{0.726}$$

where BMR is in Watts and body mass (M) is expressed in kg.

RESULTS

The first table summarizes the results of the seven species we have been working on, in collaboration with Dr. D.M. Bryant from Stirling University, Dr. H.U. Reyer from the Max Planck Institut für Verhaltensphysiologie, Seewiesen, and Dr. J.H. van Balen and Dr. J.A.L. Mertens from the Institute for Ecological Research, Arnhem. Data on ADMR (average daily metabolic rate in multiples of the BMR) are presented in two stages of the breeding cycle, incubation and nestling rearing. In the incubation phase only females were measured, and in general ADMR is lower than during the nestling phase. The one exception is the Swallow, and interestingly this species differs from the others in two respects: it is an open nester, and the female incubates alone unassisted by the male. In the House Martin, Sand Martin and Starling the male warms the eggs during the foraging absence of the female thus reducing the costs she must meet upon return, and in the Blue Tit interruptions of incubation are minimized by the male feeding the female at the nest (Haftorn, 1971). Further work is called for to quantify the contribution of each of these features to the energy budget.

In general ADMR reaches the highest level in the nestling rearing stage. This does not necessarily mean that energy constraints are less during incubation. Then, though the demands are lower, the time to meet these demands is shorter. A House Martin has to collect a net energy of 14 KJ per hour foraging during incubation and 13 KJ per hour foraging during rearing. For the Starling these figures are very close to each other as well, resp.:

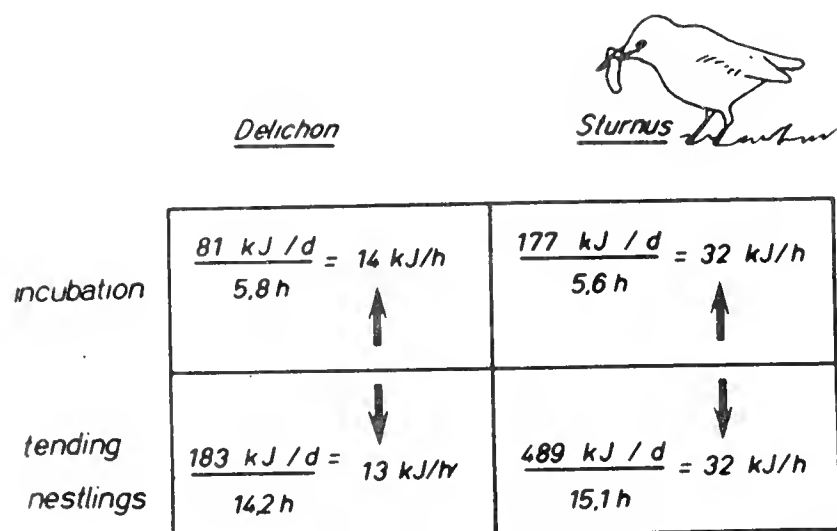


Fig. 1. Comparison of food collecting rates by incubating and nestling-rearing parents of the House Martin (left) and Starling (right), as deduced from determination of the total daily requirement and the observed time budget of the parents (see text)

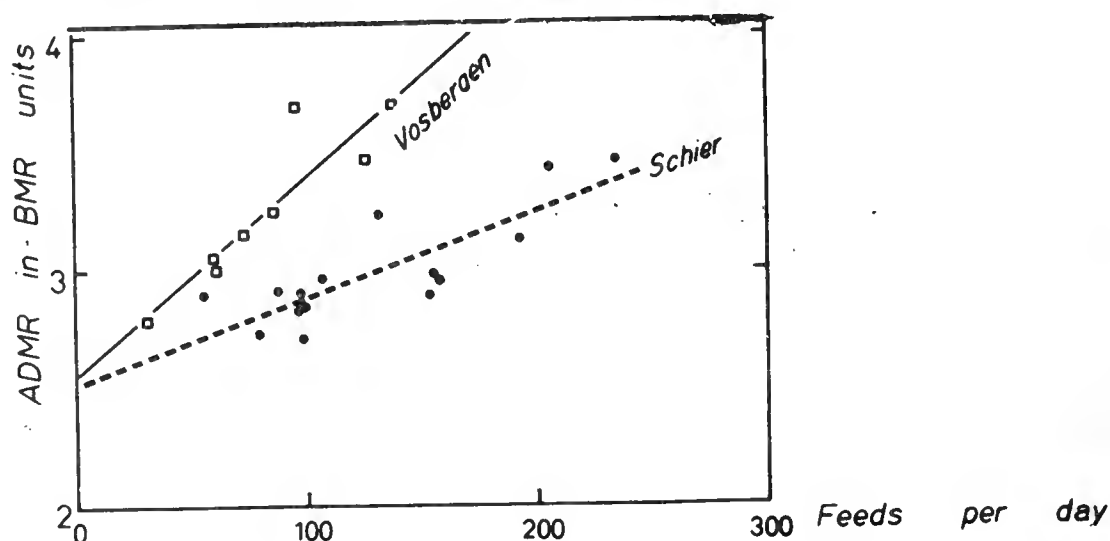


Fig. 2. ADMR (average daily metabolic rate) of parent Starlings feeding nestlings at two colonies (Vosbergen and Schiermonnikoog). Each point represents the outcome of a $D_2^{18}O$ measurement plotted in relation to the number of feeds the parent delivered that day

32 and 32 KJ h^{-1} (Fig.1) (capture rate is here calculated as the quotient of total daily energy expenditure and time spent foraging).

The energy expenditure of nestling rearing Starlings is strongly influenced by foraging conditions, which differed markedly in between our two study colonies. In the Vosbergen colony feeding rates were low and feed size was large (Westerterp et al., 1982) compared to Schiermonnikoog (Tinbergen, 1981). On Schiermonnikoog, parental energy expenditure per feed was less than half that in the Vosbergen, where the parents had to cross a woodland zone before reaching the feeding area (Fig.2). Differences in cost of parental care are thus the result of differences in time devoted to flight, the most expensive behaviour category.

The energy expenditure of flight was studied in more detail by plotting daytime MR as a function of flight time (Fig.3). Daytime MR was calculated from ADMR by subtracting overnight MR. For this one incubator and three nestling rearers were retrapped at dawn giving overnight MR values of resp.: 1.54, and 1.80, 1.77 and 1.89 BMR. Flight time ranged from 2.1% (incubator) to 21.6% (single parent rearer) of the active day period (5.00-21.30 h). MR was very closely correlated with flight time. Calculating flight costs and foraging (non-flight) costs from these data, for the first, we have to extrapolate more than 4 times the observed range. The resulting figures with 5% confidence intervals are flight 14.5 ± 2.1 BMR and foraging 2.48 ± 0.28 BMR.

Rearing Starlings fly at a speed of 14 m sec^{-1} , well above their optimal range speed of $6-10 \text{ m sec}^{-1}$ (Tucker, 1974; Norberg, 1981a). Observations in

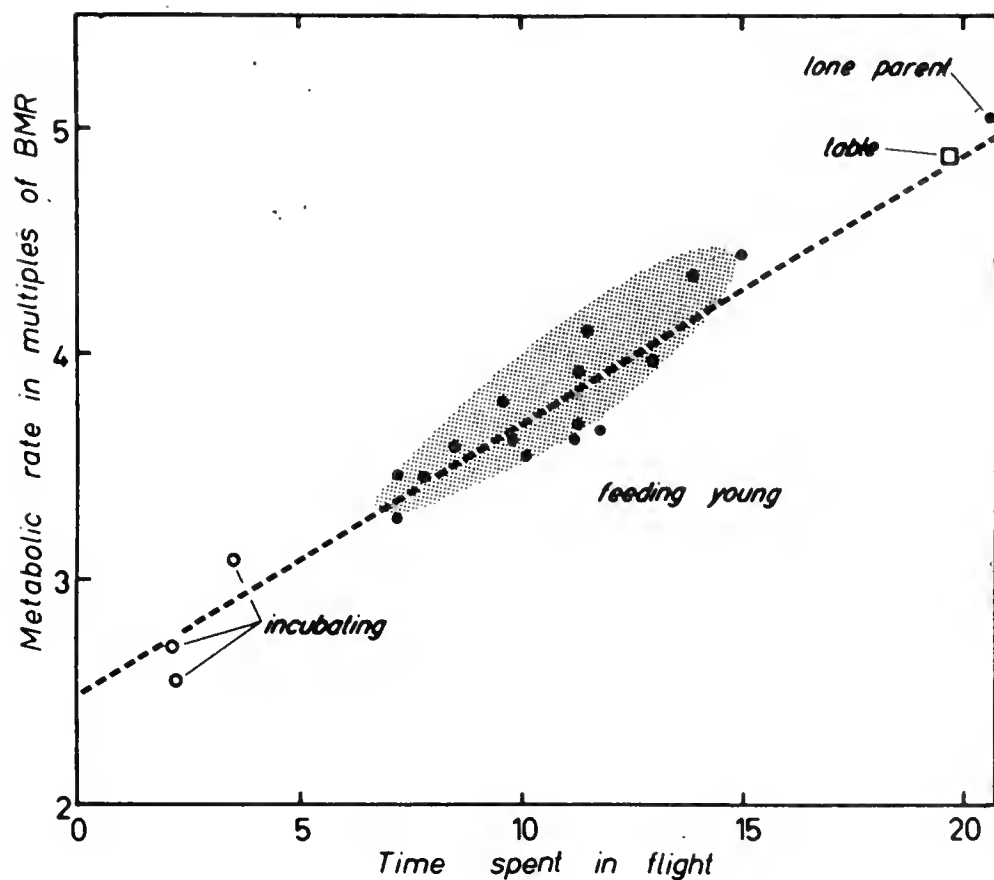
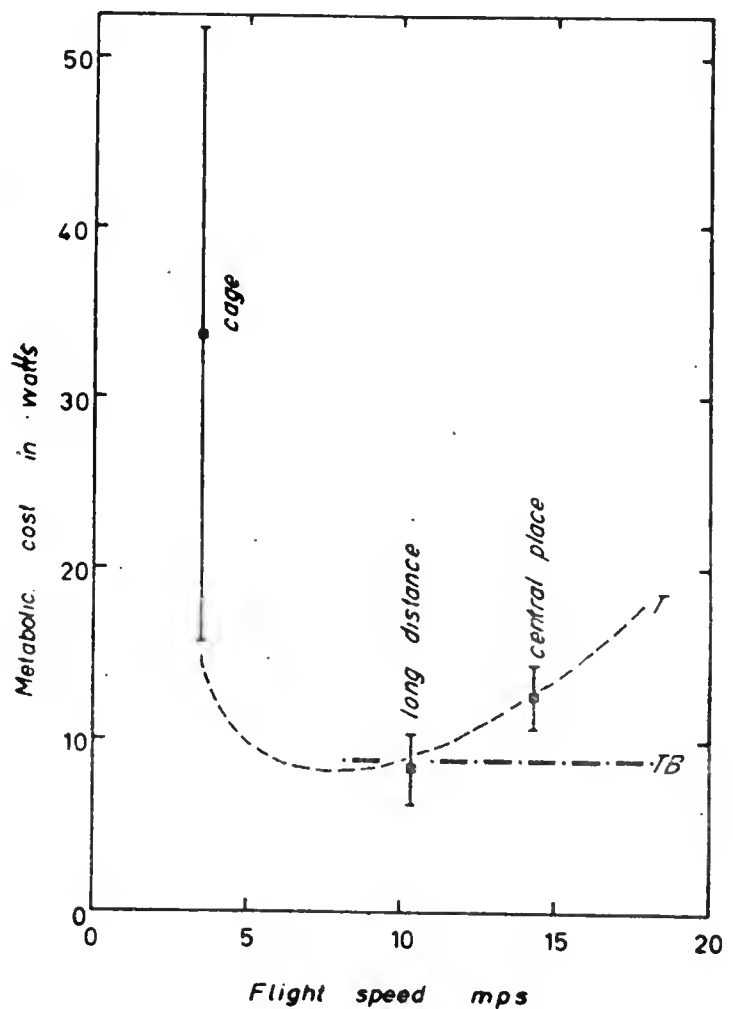


Fig. 3. Metabolic rate in breeding Starlings in relation to the per cent of time devoted to flight. Each point represents the outcome of a simultaneous $D_2^{18}O$ determination coupled with time-budget observation (see text for details)

Fig. 4. Metabolic cost of flight in relation to flight speed in the Starling, as deduced from $D_2^{18}O$ determinations in three situations: parents feeding young at the nest ("central place"), parents displaced from the nest and homing from 10-30 km ("long distance"), and non-parents confined to a small outdoor cage ("cage") making short flights. Means and 95% confidence interval are shown. Included is the empirical value obtained by Torre-Bueno in windtunnel experiments (TB, valid for range of speed shown) and the theoretical expectation according to Tucker's formula (both from Torre-Bueno, Larochelle, 1978)



Starlings flying at a lower speed of 10 m sec^{-1} , 4 birds which were displaced 10-30 km from their nestbox, resulted in a flight figure 4 of $12.1 \pm 0.3 \text{ BMR}$. This figure is very close to the $11.1 \pm 1.2 \text{ BMR}$ measured by Torre-Bueno and Larochelle (1978) in 90 min windtunnel flights of Starlings.

In the foraging cages flight speed was 3.5 m sec^{-1} , well below the optimum. Again MR was closely related with flight time, ranging from 0-4% of the

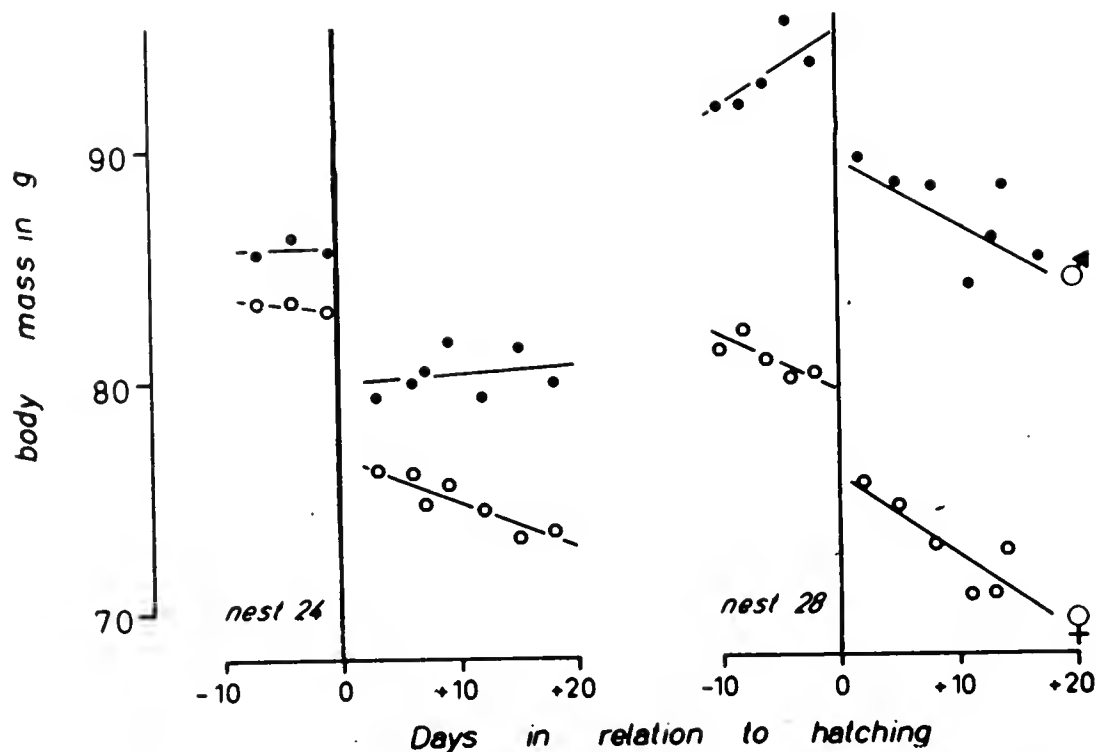


Fig. 5. Detailed records of changes in body mass of parent Starlings at two nests equipped with a balance, in relation to the day of hatch

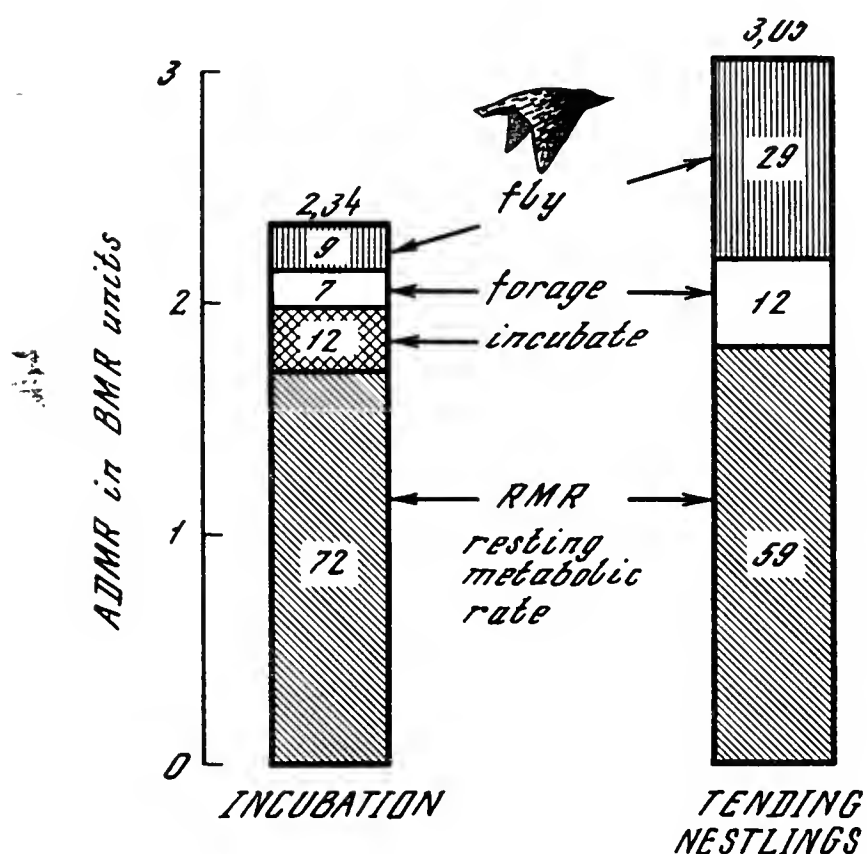


Fig. 6. ADMR of the hen Starling in two phases of the breeding cycle, expressed in BMR units, as determined by $D_2^{18}O$ measurements of free-living subjects. The components of the energy budget are found by difference measurements; the figures within the blocs designate percentual contribution to the total daily metabolism

6-10 h observation period. Extrapolating to 100% flight we get a figure of 39.0 ± 20.7 BMR! In figure 4 the three estimates of flight costs are plotted against flight speed, showing good agreement with the theoretical model of Tucker (1974). MR in this figure is expressed in W using a BMR value of $0.868 W$, the BMR of a "normal" Starling of 77.5 gram.

We are now in a position to compare energy budgets of the parent Starling in two phases of the breeding cycle (Fig. 6). The component "resting metabolic rate" requires explanation. RMR includes all night activities, as we have no assessment of nocturnal costs for non-breeding Starlings. Thus RMR for the incubation phase includes the increment of overnight incubation (estimated to be negligible in the range of air temperatures concerned, on the basis of Biebach's measurements in this colony) and includes the costs of flight to and from the roost for the nestling tender. For the RMR during the day empirical measurements are available from birds held in the outdoor foraging

T a b l e 1. ADMR in BMR units for seven species during incubation and tending nestlings

| Species | | Incubation | n | Tending nestlings | n | Source |
|--------------|------------------|------------------------|---|-------------------|----|--------------------|
| Sand martin | Riparia riparia | 3.60±0.04 ¹ | 3 | 4.34±0.18 | 10 | Westerterp, Bryant |
| House martin | Delichon urbica | 2.94±0.02 | 3 | 3.82±0.07 | 39 | Bryant, Westerterp |
| Swallow | Hirundo rustica | 4.03 | 1 | 3.90±0.18 | 14 | Westerterp, Bryant |
| Blue tit | Parus caeruleus | 3.48±0.29 | 4 | 3.87±0.05 | 2 | Bryant |
| Great tit | Parus major | | | 2.94±0.20 | 13 | Westerterp, Bryant |
| Starling | Sturnus vulgaris | 2.36±0.06 | 6 | 3.11±0.06 | 26 | Westerterp |
| Kingfisher | Ceryle rudis | | | 4.26±0.17 | 13 | Westerterp, Reyer |

¹ Mean values are followed by standard errors

cages (by extrapolation from time-budget data). The overnight expenditure of an incubating Starling is 1.54 BMR. Birds which go to the communal roost spend 1.82 BMR including the flight to and from. For the other components (forage and fly) the procedure is more straightforward. Since we are here concerned with the additional cost of the activity to the bird, we have for this energy budget subtracted the resting level cost factor from the activity level (the additional cost of foraging is hence the difference between 2.48 BMR of the foraging bird and the daytime resting level and the additional cost of flying is the difference between 14.5 BMR of the flying bird and the daytime resting level of 1.80 BMR). These new factors for the additional cost of the activity can now be combined with time budget data to yield added cost incurred when the parent reaches the decision to engage in that activity (in this view we consider that the parent does not have the option of reducing the resting expenditure but must face this as an unavoidable background level of expenditure). Incubation cost (during the daytime) is thus obtained by subtracting all the other components (BMR, fly and forage) from the total energy expenditure of the incubating hen (given in Table 1). Clearly flight is quantitatively the most important portion of the energy budget that can be influenced by behavioural decisions of the parent, and we should consider modes of economizing on this activity. Norberg's (1981b) suggestion that flight expenditure might be reduced by lowering body mass at critical junctures seems worth following up, and we will examine changes in the body mass of parent Starlings in relation to the reproductive cycle as a prelude to further empirical analysis of parental investment.

Starlings indeed minimize body mass by reducing their body reserves in the most active part of the season, when food is abundant. In winter they can carry up to 25 grams of fat (Ward, 1977). As soon as the breeding activity starts in early March, with nest occupation and pair formation, body mass drops (Fig.7). There is a small increase in males after settling and of course the females show a sharp increase just before laying. Body mass remains more or less constant during incubation but drops suddenly 4-6 grams at hatching (Fig.5), coinciding with an increase in time spent flying. Carcass analysis on 7 males and 8 females revealed that the main part of this mass

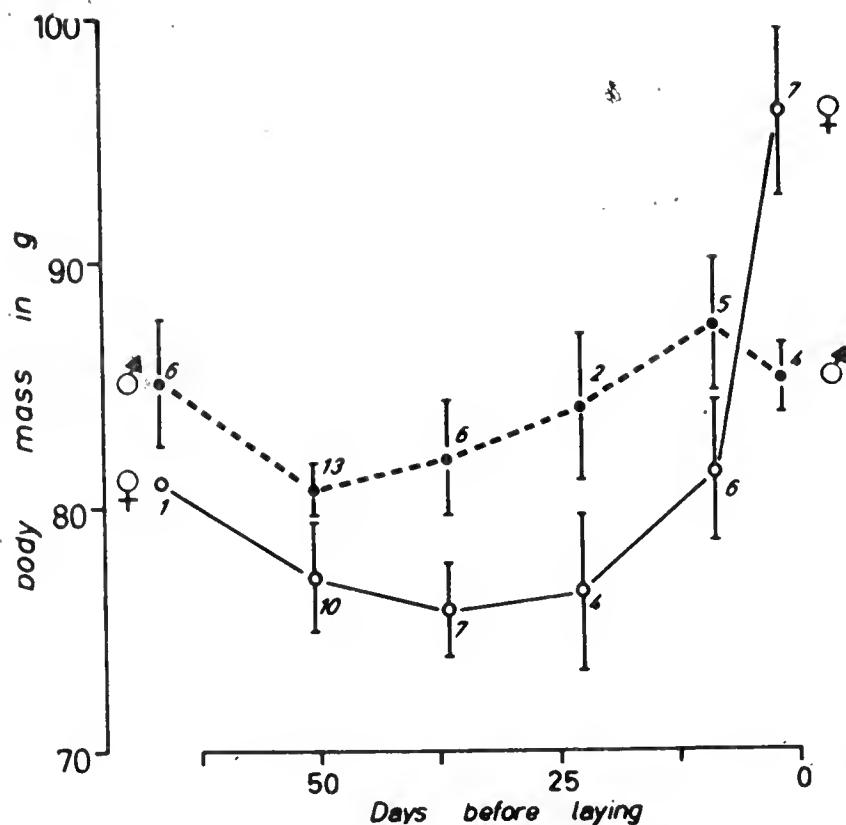


Fig. 7.

Changes in body mass of parent Starlings (sex indicated) in the pre-laying period. Means, 95% confidence intervals of the means and sample sizes are shown

change is a result of mobilizing body fat. During the nestling stage body mass generally declines further, the fall being greatest when large broods are raised (Westerterp et al., 1982). In view of the many similarities with Pinowska's (1979) analysis of body mass change in breeding House Sparrows and van Balen's (1973) observation in breeding Great Tits, including the body mass fall at hatching, the pattern described here for the Starling may be a more general one. The next step will be to measure flight cost empirically in relation to body mass changes in the same individual, to confirm the supposition that mass reduction entails a substantial saving in flight cost.

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TIME AND ENERGY IN AVIAN INCUBATION

Carol Masters Vleck

Department of Ecology and Evolutionary Biology,
University of Arizona, Tucson, Arizona 85704, USA

Incubation of eggs is an important part of the avian reproductive cycle and is potentially expensive in terms of both time and energy. With few exceptions (Kendeigh, 1940, 1952, 1963; Skutch, 1962) there were few studies on the physiology and energetics of incubation until interest was sparked by the investigations of Drent and co-workers (Drent, 1970; Drent et al., 1970). Subsequent studies have begun to provide answers to some of the fundamental questions in this area. Drent (1975) provides a comprehensive review of data then available. I will briefly review some recent studies and attempt to show how the activity of incubation affects time and energy budgets in free-living birds.

ENERGY COSTS OF INCUBATION

Avian eggs must be kept warm (32-38°C) if they are to develop and hatch successfully. For birds that warm their eggs by sitting on them most of the necessary heat input comes from the adult's metabolism. One approach to estimating the energy cost of incubation has been through construction of simple linear heat flow models (Kendeigh, 1963; Ricklefs, 1974). Although such models can predict the heat input required to maintain egg temperature (Drent, 1970), they do not provide good estimates of the metabolic cost to an adult birds of incubation (Vleck, 1981a). The heat flow models that have been used ignore two important factors. First, heat produced as a byproduct of the normal metabolism of an incubating adult might substitute for at least part of the heat needed to maintain egg temperature (King, 1973). Second, a bird that returns to incubate at a cold nest must expend additional energy to rewarm the eggs.

The energy cost of maintaining eggs at incubation temperature can be measured directly as the difference between metabolic rates of incubating and non-incubating birds under otherwise similar conditions. Metabolic rate (measured as rate of oxygen consumption) of incubating Zebra Finches (Poephila guttata) is about 20% higher than that of birds roosting in a nest but not incubating, when nest temperatures are below the lower critical temperature of about 28°C. Above 28°C there is no significant increment in energy expenditure for incubation (Vleck, 1981a). In Zebra Finches, the cost of maintaining incubation temperature is lower than that predicted by the heat flow models of Kendeigh (1963) and Ricklefs (1974) at most nest temperatures, indicating that at least some of the heat necessary to maintain egg temperature is a byproduct of the bird's normal metabolism, as King (1973) suggested.

Direct measures of the cost of steady-state incubation are available for three other species. In Starlings (Sturnis vulgaris) oxygen consumption during incubation is 20-25% greater than for non-incubating birds at temperatures below the lower critical temperature (about 28°C) (Biebach, 1979). The cost of incubation increases with clutch size in Starlings (Biebach, 1981). Starlings have a relatively larger clutch and a relatively higher cost of incu-

bation than do Zebra Finches. In American Kestrels (Falco sparverius), metabolic rate increased in one of three individuals during incubation but did not change significantly in the other two (Gessaman, Findell, 1979). The authors of this study suggest the differences may have been due to differences in nest insulation, but did not measure this variable. Mertens (1980) measured heat flux from nest boxes of Great Tits (Parus major). At ambient temperatures less than 20°C, heat loss from boxes containing incubating females averages 1.5 to 2 times the heat loss from boxes containing a nest and a non-incubating female.

Available data suggest that within the thermal neutral zone, heat needed for incubation can come from the bird's normal heat production and there is little or no incremental energy cost required to keep eggs warm. However, below the lower critical temperature, the clutch of eggs functions as a poorly insulated extension of the bird's own body. Consequently, the conductance of the bird-egg complex exceeds that of non-incubating birds and metabolic rate must be increased to maintain homeothermy.

Rewarming eggs that have cooled during parental absence from the nest is an additional energy expense in incubation. Metabolic rates of incubating Zebra Finches (Vleck, 1981a) and Starlings (Biebach, 1979) increase more than twofold when the eggs in their clutches are artificially cooled. When Ptarmigan (Lagopus lagopus) resume incubation of cooled eggs, heart rate increases fourfold until the eggs reach incubation temperature (Gabrielsen, Steen, 1979). This tachycardia is presumably associated with increased heat flow to the incubation patch, and must entail an increase in rate of energy expenditure by the adult.

Because the rate of energy expenditure during rewarming eggs is higher than during steady-state incubation, the total energy cost of incubation is influenced by the pattern of adult attentiveness at the nest as well as by nest structure and ambient conditions. In a Zebra Finch nesting at an ambient temperature of about 25°C the cost of rewarming eggs increased the average cost per hour on the nest by about 8% over the cost of continuous incubation. Such costs would increase as ambient temperature declines or attentiveness becomes more fragmented (Vleck, 1981a).

Behavioral changes associated with incubation may partially or fully compensate for the energy costs of keeping the eggs warm. A bird sitting in an insulating nest should have reduced radiative and convective heat loss compared to a bird perched in the open. Walsberg and King (1978a,b) estimate that the rate of energy expenditure of three species of birds that nest in open cups (Agelaius phoeniceus, Empidonax traillii, and Zonotrichia leucophrys) should be 15-18% less when they are in a nest than when they are perched in the open because of the increased thermal resistance of the nest. They suggest incubating birds may actually be at an energetic advantage because the effects of nest microclimate and insulation can more than compensate for the additional heat expended to warm the eggs. Daily energy expenditure can also be reduced during incubation if time spent in energetically expensive activities such as flight is reduced. In House Martins (Delichon

urbica) energy expended during incubation is significantly less than that used during the nestling period because so much less time is spent in flight (Bryant, Westerterp, 1980).

TIME COSTS OF INCUBATION

The time that a bird spends incubating its eggs is unavailable for foraging and other activities. In many cases time allocated to incubation may have a greater impact on a bird's energy balance than does the energy expended to supply heat to the eggs. Patterns of attentiveness, or time spent incubating the eggs, can be viewed as evolutionary resolutions of the conflict between individual maintenance behavior and parental care. Maximizing attentiveness may increase the precision with which a bird can regulate incubation temperature and provide optimal conditions for development of the eggs, whereas reducing attentiveness provides more time for foraging and self-maintenance. Attentiveness patterns of incubating birds illustrate a diversity of solutions to this conflict (White, Kinney, 1974; Skutch, 1976).

Attentiveness patterns and egg temperatures of 9 species of birds, all nesting in a single habitat, are summarized in Table 1. In five of these the female does all of the incubating, and during incubation forages for herself. Females of these species were on the nest for only 63-75% of the daylight hours, so average egg temperature during the day was lower than at night, despite higher ambient temperatures. The Starling and House Martin display similar patterns of attentiveness and egg temperature (Prinzinger et al., 1979). Although overall attentiveness is comparable, the duration of bouts of attentiveness and absence were much shorter in the small hummingbirds than in the larger oriole and finch. Attentiveness is higher and egg temperature less variable in species in which the male assists by feeding the female at the nest. In two species in which both sexes incubate, the attentiveness is nearly 100% and incubation temperature varies only a few tenths of a degree over an entire day, yet each member of the pair may have half of their daylight hours free.

When foraging time is reduced by incubation duties, either food intake must decrease as found in incubating Black-billed Streamtails (Trochilus scitulus) (Schuchmann, Jakob, 1981) or foraging efficiency must increase. Male Panterpes insignis hummingbirds allow females to nest within their defended territories and feed at the richest sites therein, thus enhancing foraging efficiency of the nesting female (Wolf, Stiles, 1970).

In some species safety margins are so small that foraging time and food intake may sometimes be insufficient to permit normal incubation. Embryos of such species can often tolerate interruptions in incubation. When food is short Fork-tailed Storm-Petrels (Oceanodroma furcata) remain at sea and do not incubate (Simons, 1981), yet their embryos can survive cooling to near-freezing temperatures and begin development again when rewarmed (Vleck, Kenagy, 1980). When inclement weather limits foraging time of incubating female hummingbirds, they allow body temperature and egg temperature to drop at night in order to maintain energy balance (Calder, Booser, 1973; Vleck, 1981b).

Clearly, time and energy are linked resources. A more complete understanding of the energetic effects of time allocations to incubation must await

T a b l e 1. Attentiveness and incubation temperature of birds nesting in California chaparral for species in which the female alone incubates, the male assists the female to a limited extent, and in which both sexes share duties approximately equally. Attentiveness and egg temperature are expressed as mean \pm standard deviation. (For methods see Vleck, 1981b)

| Species | Total hours analyzed | Daytime attentive- ness (%) | Mean bout length (min) | | Mean temperature (°C) | | | | |
|----------------------------------|----------------------------|-----------------------------------|---------------------------|--------|-----------------------|------|-----------|------|--|
| | | | Atten- tive | Absent | Daytime | | Nighttime | | |
| | | | | | Egg | Air | Egg | Air | |
| <u>Female only</u> | | | | | | | | | |
| Archilochus | | | | | | | | | |
| alexandri | 120 | 69.9± 8.5 | 6.3 | 2.3 | 31.6±2.2 | 15.2 | 33.8±1.8 | 11.0 | |
| Calypste anna | 110 | 74.6± 8.8 | 8.1 | 3.0 | 34.9±1.9 | 10.8 | 36.8±1.4 | 6.1 | |
| Empidonax | | | | | | | | | |
| difficilis | 36 | 62.7±17.6 | 14.5 | 8.6 | 34.3±0.8 | 15.0 | 34.3±1.1 | 12.7 | |
| Icterus | | | | | | | | | |
| galbula | 84 | 63.1±19.1 | 30.1 | 17.4 | 32.6±2.6 | 18.9 | 34.0±2.1 | 11.1 | |
| Pipilo eryth- ropthal- mus | 78 | 67.0±14.0 | 41.4 | 20.4 | 37.0±1.2 | 19.4 | 38.0±0.7 | 10.6 | |
| <u>Male assists</u> | | | | | | | | | |
| Psaltriparus | | | | | | | | | |
| minimus ¹ | 254 | 54.5±12.6 | 11.8 | 10.5 | 34.7±1.7 | 17.3 | 35.9±0.7 | 7.3 | |
| Carpodacus | | | | | | | | | |
| mexicanus ² | 68 | 72.7±20.1 | 19.9 | 7.5 | 31.8±2.1 | 17.4 | 32.5±0.6 | 14.4 | |
| Carpodacus | | | | | | | | | |
| mexicanus ² | 5 | 88.0± 3.6 | 17.6 | 2.4 | 35.5±1.2 | 18.9 | - | - | |
| <u>Male shares</u> | | | | | | | | | |
| Zenaida mac- | | | | | | | | | |
| roura | 61 | 100 | - | - | 37.0±0.6 | 16.1 | 36.7±0.8 | 14.0 | |
| Toxostoma re- | | | | | | | | | |
| divivum | 24 | 99.5 | - | - | 38.0±0.6 | 15.0 | 37.9±0.3 | 7.7 | |

¹ The male was seen entering the covered nest but probably does not incubate.
² The male feeds the female on the nest.

further study. It is clear that if such a study is to be successful, it must encompass aspects of avian biology far beyond incubation alone. We are beginning to understand some of the costs of incubation in terms of time and energy, but as yet we have a limited ability to integrate these into a more complete understanding of time and energy budgets of free living birds.

ACKNOWLEDGEMENTS

Portions of this research were supported by a Frank M. Chapman Grant from the American Museum of Natural History.

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THE ENERGY REQUIREMENTS OF TERRESTRIAL LOCOMOTION IN BIRDS

James R. King

Department of Zoology, Washington State University,
Pullman, WA 99164, USA

Except during migration, birds that forage on the ground typically spend much more of their active day engaged in bipedal locomotion than in flying. This is of course mandatory in flightless species such as ratites and penguins, obvious in various strongly cursorial species such as galliforms, but less obvious in other kinds of ground-foraging birds. A few examples, however, will illustrate the reliance by diverse species on terrestrial locomotion. Black-billed Magpies (Pica pica hudsonia) engage in walking or running for 13-18% of their active day in autumn and as much as 26% during the breeding season (Mugaas, King, 1981). Brown Thrashers (Toxostoma rufum) in winter occupy 46-48% of their active day in terrestrial locomotion associated with foraging, but spend only 0.2-0.5% in flight (Fischer, 1981). A bird of a still different life style, the Spotted Sandpiper (Actitis macularia), spends 17-59% of its active day in "walking and foraging" but only 2-4% in flight during the breeding season (Maxson, Oring, 1980). The well-known overland treks by penguins between the sea and their breeding colonies (commonly 100 km or more: e.g., Budd, 1962) are, of course, an extreme case of avian dependence on terrestrial locomotion.

The foregoing examples illustrate that terrestrial locomotion occupies a large fraction of the daily time budgets of many birds. In converting time budgets to energy budgets it is therefore important to include terrestrial locomotion as an explicit component and to estimate its metabolic cost as accurately as possible. This is especially crucial if the objective is to estimate cost/benefit ratios, as in the examination of theories of optimal foraging.

Estimating the metabolic cost of terrestrial locomotion for ecological purposes is not as simple and straightforward as it may seem superficially. In the account that follows, I attempt to (1) inventory existing data and sources of information, (2) outline pitfalls and practical problems, and (3) highlight useful lines of future inquiry.

MEASUREMENTS OF POWER CONSUMPTION WHILE RUNNING

Taylor et al. (1982) analyzed the oxygen consumption of 14 species of birds (0.042-103 kg) running on a motor-driven treadmill within their apparent thermoneutral zones. The total power consumption while running in all except species that waddle (geese, penguins) conforms closely to the equation

$$W \text{ kg}^{-1} = 5.6(\text{kg})^{-0.246} + 11.4(\text{kg})^{-0.285} \cdot \underline{v} \quad (1)$$

where \underline{v} = treadmill velocity in m s^{-1} . The first addend on the right expresses the allometric dependence of the Y-intercept (power consumption extrapolated to zero speed) on body mass. The first term of the second addend expresses the body-mass dependence of the minimal cost of transport $J(\text{kg} \cdot \text{m})^{-1}$. When multiplied by velocity this yields the net power consumption of locomotion alone at the stated velocity. Power consumption by birds that waddle is slightly greater than in the others, presumably because of the side-to-side motion of the body (Pinshow et al., 1977).

Equation 1 supplies the baseline for estimating power consumption by free-living birds when they are walking or running. Because the experimental conditions supplying the data for this equation were designed for other than ecological extrapolations, however, its use for such purposes must be tempered by a clear understanding of its limitations. These spring from potential artifacts of locomoting on a treadmill and from the poorly known effects of environmental temperature on total power consumption when running. Many of the artifacts are apparently small and can be disregarded, but others may be important and cannot be overlooked in extrapolating laboratory data to field conditions. In doing so, ecologists should be wary.

SOME POTENTIAL ARTIFACTS IN TREADMILL RUNNING

Locomotion on a moving vs. stationary surface and smooth vs. irregular surfaces

It is not difficult to imagine that running on a treadmill involves neuromuscular reactions that differ from those on a stationary natural surface. In fact, Wetzel et al. (1975) found small differences in the patterns of limb flexion between cats running on a motor-driven treadmill and those running on a smooth floor. Whether this difference is great enough to be reflected in power consumption is moot, but it seems likely that the error would be small. In addition to moving, a treadmill belt is smooth, unlike irregular natural surfaces. Locomoting across an irregular surface requires stride-by-stride adjustments of stride frequency and length. Such adjustments may increase power consumption above that on a smooth treadmill at the same average velocity. This may, in fact, explain why White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) locomoting on a wire-mesh substrate consume 15% more power at low speeds and 36% more power at high speeds than predicted by equation 1 (F.V. Paladino, unpublished data). Experiments with additional species must be conducted to learn if this result can be generalized.

Absence of wind resistance

An animal on a treadmill is typically stationary in air and not subject to the expenditure of "parasite power" to overcome aerodynamic resistance. In a biped the size of man running at middle speeds the parasite power consumption amounts to only 7-8% of total power consumption (Pugh, 1971). In small animals and at slower speeds the parasite power requirement is less and can be disregarded (Alexander, 1976) except in large, swift cursorial birds. The effect of relative windspeed on convective heat transfer, however, may be more significant, as will be mentioned later.

Steady vs. intermittent locomotion

Ground-foraging birds do not move steadily for long periods, as on a treadmill, but typically move intermittently through short distances, unlike the invariant speed and steady-state oxygen consumption on a treadmill. For instance, it can be computed from the data of Cody (1971) from several species of finches foraging in winter flocks that individuals that move about 0.67 km h^{-1} (without flying) are stationary for 80-90% of the time, and move intermittently at $0.4-1.6 \text{ km h}^{-1}$. Because oxygen consumption is commonly greater during the first few seconds or minutes of running than later (Taylor et al., 1982), although not always so (Bamford, Maloiy, 1981), the average

cost of intermittent locomotion is likely to be slightly greater than the steady-state cost. Empirical measurements are needed to learn if the discrepancy is significant.

EXTERNAL WORK AND UPHILL/DOWNHILL MOVEMENT

I will define external work (\underline{W}) as work done on the environment in overcoming frictional resistance with the substrate, counteracting aerodynamic drag (as already discussed), and moving upward ($+\underline{W}$) or downward ($-\underline{W}$) in the gravitational field. Work done against potential and kinetic forces within the body is also sometimes called "external work" in a biomechanical context (Cavagna et al., 1976) but ultimately appears as heat production (\underline{H}) in an animal in a steady-state. Metabolic power consumption (\underline{M}) is related to heat and work through the familiar equation $\underline{M} = \underline{H} + \underline{W}$ (e.g. Nielsen, 1970). In men walking on a horizontal motor-driven treadmill $\underline{M} = \underline{H}$, and no external work can be detected (Snellen, 1960). The only significant positive work by walking animals apparently involves lifting mass against gravity, or conversely when moving downhill (negative work). Snellen (1960) showed that the increment of \underline{M} in men walking on an inclined treadmill matched the work of lifting the body, as estimated from the equation

$$\underline{W} = \underline{a} \cdot \underline{b} \cdot \underline{v} \cdot \sin \theta \quad (2)$$

where \underline{b} is the body mass in kg, \underline{v} is velocity in m s^{-1} , θ is the angle of inclination in degrees, and \underline{a} is a proportionality constant (9.807) converting kg-m to joules. Since \underline{v} is expressed in m s^{-1} , \underline{W} is in J s^{-1} , or watts.

As is evident from equation 2, and as shown empirically by Taylor et al. (1972) in mammals, the cost of running uphill is directly proportional to body mass, speed, and the sine of the angle of ascent. The ratio of the increment of work when ascending (expressed as metabolic cost, $\Delta \underline{M}_\theta$) to power consumption when moving horizontally (\underline{M}_0) at a speed corresponding to the maximum oxygen consumption ($\underline{V}_{O_{2\max}}$) can be estimated by the ratio of equation 2 to equation 1 if the equation for speed at $\underline{V}_{O_{2\max}}$ ($\text{m s}^{-1} = 2.43 \text{ kg}^{0.122}$, Taylor et al., 1981) is substituted for \underline{v} in both equations:

$$\Delta \underline{M}_\theta / \underline{M}_0 = 0.71 \cdot \sin \theta \cdot (\text{kg})^{0.30} \quad (3)$$

At top speed (the only similar speed available for scaling the ratio to body mass), a 22-g bird such as a Chaffinch spends 11% more energy in climbing a 30° slope than running horizontally at the same speed, and a 22-kg Greater Rhea spends 89% more. At 60° these estimates increase to 20% for the Chaffinch and 155% for the rhea. At the much slower speeds at which birds typically move, however, the work increment is less and may be negligible in relation to other sources of error. For instance, work by a 22-g Chaffinch moving up a 30° slope at 0.3 m s^{-1} (1.1 km h^{-1}) augments metabolic power consumption by about 6% compared to consumption at the same speed when running horizontally.

If an animal ascends and descends to its initial elevation using the same path and speed it may spare as much metabolic energy in descending as was spent ascending (cf. Taylor et al. 1972 on 4-legged runners). Use of different paths and speeds will produce various ratios of cost and recovery that cannot be explored in the space available here. An additional complication arises from the observation that men descending treadmill slopes of 18%

(ca. 10°) or more spend more metabolic energy per unit distance than in moving horizontally (Margaris, 1976). It is unknown if smaller bipeds such as birds react in the same way.

THERMOREGULATORY COMPLICATIONS

The measurements used in computing equation 1 were conducted within the apparent thermoneutral zones of the birds involved, and are therefore thought to be uncomplicated by an increment of thermostatic heat production. An environment that is "thermoneutral" for an immobile bird, however, is not necessarily so for a moving one, since the movements of the limbs and body increase convective heat loss even in still air (Winslow, Gagge, 1941). Furthermore, convective heat loss is accentuated in proportion to $v^{0.5}$ as a bird moves through air, or air moves past a bird (Robinson et al., 1976). With but few exceptions, studies of animals on treadmills have not included the use of a fan to match airspeed to treadmill speed. In one investigation of a 22-kg Greater Rhea in which a fan was used (Taylor et al., 1971) it was later reported (Fedak et al., 1974) that oxygen consumption was not measurably different when the fan was on or off. In smaller birds, however, convection is a more prominent component of the heat budget. For instance, oxygen consumption by immobile White-crowned Sparrows (27 g) increases by 7.8%, compared to its value in still air, when windspeed is 0.14 m s^{-1} (equivalent to slow walking) and air temperature is 1°C , and by 13.5% when windspeed is 0.42 m s^{-1} (fast walking). In warmer air (20°C) the corresponding values are 6.7% and 12.3% (Robinson et al., 1976). These rough estimates indicate that power consumption can be significantly augmented by a bird's self-convection while moving through still air, and that conventional treadmill studies of small-bodied animals will underestimate total power consumption of free-living individuals by a corresponding amount unless the range of adjustment by insulation is sufficient to compensate for the added convective loss and/or the heat increment of locomotion substitutes for it. This remains to be shown by future investigations.

Whether or not the heat increment of locomotion substitutes for part or all of the thermostatic requirement in the cold has been controversial for decades. There is not space in this brief report to review the evidence pro and con, but only to sketch some new results. On the basis of indirect evidence, Ketterson and King (1977) hypothesized that the heat production of voluntary locomotor activity substituted for thermostatic heat production in White-crowned Sparrows exposed to cold temperatures. Results obtained later by F.V. Paladino (to be reported in detail elsewhere) are consistent with this hypothesis. At air temperatures below the thermoneutral zone the slope of the regression of oxygen consumption on treadmill speed in White-crowned Sparrows progressively decreases with decreasing air temperature and becomes zero at about -10°C . At this air temperature thermostatic substitution is apparently complete, and a White-crowned Sparrow would spend no more energy in moving around while searching for food than it would spend just sitting still and shivering to produce thermostatic heat. In effect, locomotion costs nothing. This has important implications in the estimation of cost-benefit ratios in the economics of foraging (e.g., Pyke, 1981).

SUMMARY

Birds that forage on the ground spend much more time, except during migration, in terrestrial locomotion than in flight. In converting time budgets to energy budgets it is therefore desirable to estimate the energy cost of locomotion, especially if attempting to understand cost/benefit ratios in foraging. Data for estimating power consumption in terrestrial locomotion are available only from birds moving on a horizontal treadmill in the thermoneutral zone. The main purpose of this report is to evaluate the errors involved in extrapolating from laboratory data to field conditions. Treadmill studies are ecologically unrealistic because (1) there is no wind resistance (small error) or forced convection of heat (significant error) in stationary animals that do not move through air, (2) running on a smooth treadmill differs from running on an irregular natural surface (potentially a significant error), and (3) moving on a treadmill at steady speed differs from intermittent movement in the field (unknown error but probably small).

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TIME AND ENERGY BUDGETS IN WINTERING TETRAONIDAE

R.L.Potapov, A.V.Andreev

Zoological Institute of the USSR Academy of Sciences, Leningrad, USSR;
Institute of Biological Problems of the North, Far-East Scientific
Centre of the USSR Academy of Sciences, Magadan, USSR

The process of determining of energy parameters in wintering Tetraonidae under natural conditions is based on some ecological features, which help in attending correct results. These are: 1 - minimal moving activity and staying of most of the day-time in snow burrows; 2 - to collect frozen excrements out of snow burrow after bird's departure is rather easy thing; 3 - homogeneity in the winter foods of Grouse species; 4 - the rate of digestion is comparatively stable throughout the time spent in the snow; 5 - the amount of food collected in the bird's crop after evening foraging corresponds in general to the quantity of droppings wasted in the burrow. Besides all this quite a lot of data on the body mass dynamic in most grouse species is now available in literature. The typical pattern of changes in body mass is to increase attending top point up to November. Then this is followed by permanent decrease from December to March. However, a few factors cause troubles in the course of field researches. Firstly, there is no possibility to check field results in aviary directly, since nobody managed to keep birds in winter on complete natural diets in aviary. Secondly, up to now there are no good reference points to estimate the basal metabolic rate (BM), since to get a bird under basal conditions one should try to clean intestines as well as coecal guts. This operation needs long starvation of a bird which may disturb it down to stress. Thus, to determine daily energy budgets in free living Grouses may be the easiest thing, which in many other birds looks like the final goal of researches on ecoenergetics.

Statistically sufficient and reasonably reliable data are brought from collecting of excrements (droppings and coecal faeces), left after a bird took out of the snow burrow. Providing that the time which a bird spends in the Burrow is known (the parameter one can observe directly in nature), we can determine the quantity of droppings for the whole day. This operation assumes, that the rate of excretion is constant throughout the time. However, the rate of droppings excretion in active birds in the daytime is known to be 1.3-2.0 times as higher as compared with the night (Moss, 1973; Höglund, 1980; Andreev, 1982). Thus, assuming the rate of excretion is permanently constant we will probably receive slightly diminished results. However, keeping in mind that the total period of activity in wintering Tetraonidae is normally just 2.5-4 hrs, the difference between day and night metabolic rates is only 1.15-1.2 times. To measure the total amount of the coecal faeces is not a problem, since these all are excreted every morning inside or nearby the burrow. The daily amount of droppings in the middle of winter in every species is comparatively constant. Otherwise the mass of coecal faeces changes considerably, the difference being 2-3 times in the same bird in few days. In some days no coecal faeces may occur at all. Nevertheless, statistics enables to estimate some average level which is stable enough.

Estimation of the daily energy intake (GEI) is a more difficult job. Observations in nature show Grouse birds are capable to consume the total daily

foodstuff, in the course of 1.5-3 hrs of feeding activity. Moreover, in some cases the daily diet may be stored in the voluminous crop, comprising up to 15-18 per cent of the body mass. Foods filled the crop in early night are normally used up to morning. This fact enables us to count the daily food consumption, providing that the period which a bird spends in the burrow is known. Energy contents of foods and excrements have been measured by means of direct calorimetry in the oxygen bomb calorimeter. The difference between daily energy consumption and excretion is the metabolisable energy (ME), which being divided to GEI is the metabolic efficiency coefficient (MEC). Quite a bit of data give the average estimation for MEC to be 0.3. This general result leads to a comparatively simple way to find DEB by knowing only the dry mass of excrements:

$$DEB = \frac{M_d q_d + (M_c \cdot q_c)}{1 - MEC} \pm dM q_m, \quad (1)$$

where M_d - dry mass of droppings, g/24 hr; M_c - the same for coecal faeces, q_d and q_c - energy contents of both substrates, kJ/g, dM - daily change in body mass, g/day; q_m - energy content of fresh body mass. Since $MEC = 0.3$, $q_m = 25.1$ kJ/g:

$$DEB = 1.43 (M_d \cdot q_d + M_c q_c) \pm 25.1 M. \quad (2)$$

Being rather primitive this equation enables to collect lots of data having statistically significant results, suitable for interspecies comparisons.

More precisely DEB of an individual bird may be determined by summarizing its components, i.e. - basal metabolism (BM), conductance (h), the activity coefficients (Dolnik, 1980), time budget (DTB), specific heat capacity for heating frozen foods and changes in the bird's body mass.

$$DEB = K_n T_n + K_d T_d + K_a T_a + K_f T_f + h T_{nd} (t_b - t_c) + h T_a (t_b - t_a) + c \cdot M_f (t_b - t_a) \pm dM q_m \quad (3)$$

where $K_n = 1.0$ BM - staying in the burrow at night;

$K_d = 1.12$ BM - the same in daytime;

$K_a = 1.6$ BM - feeding activity;

$K_f = 12$ BM - flight;

T_n , T_d , T_a and T_f - time spent for all these activities, hrs; t_b , t_c and t_a - body, in the snow burrow and ambient temperatures; c - specific heat capacity of fresh, M_f - daily food consumption, BM, t_c and h have been already measured experimentally (see West, 1976; Andreev, 1977; Hissa et al., 1982).

Being estimated simultaneously by different methods the DEB calculations give rather similar results (Table 1). We suggest these to be close to real energy metabolic parameters in wild birds.

Investigation of DTB in wild birds along with temperatures in snow burrows show two principal features, which seem to be responsible for remarkable energy economy in free living birds. Firstly, this is deep decrease in moving activity in winter and staying most time of day in the resting attitude. Secondly, the process of staying in the snow burrow means that most part of the winter a grouse bird spends in the thermic refuge, where temperature is between -5°C and zero (Andreev, 1977; Marjakangas, 1982). In this point we encounter with some sort of a feedback: the lower ambient temperature is the

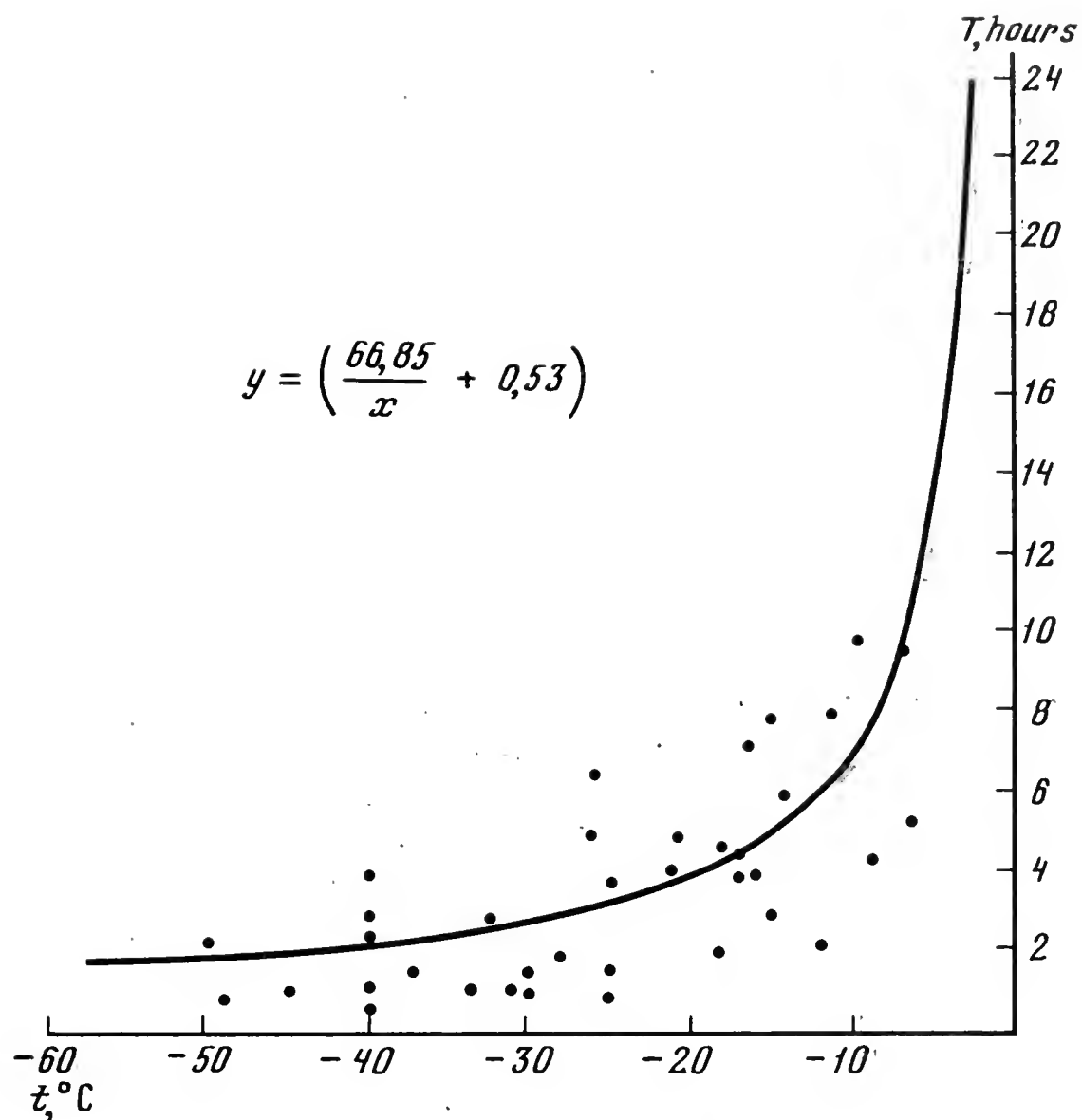


Fig. 1. Relation between ambient temperatures ($t, ^\circ\text{C}$) and the time spent by Grouses for feeding (T , hours) in mid-winter

longer bird stays in the burrow (Fig. 1). Using this relation one can find that the average ambient temperature for a Grouse in every case is actually about -7° in spite of wide range of air temperatures, which fluctuate from -10° to -50°C or even more. In other words, by using snow burrows and varying resting time a grouse bird can principally increase the ambient tem-

Table 1. Time and energy budgets demensioned on observations and measurments in nature

| Species, sex | W_b | Time budgets, h | | | | dw, g | DEB, kj/day | |
|---------------------------------|-------|-----------------|-------|-------|----------|-------|-------------|-------------|
| | | T_n | T_r | T_a | T_{fl} | | -20° | -40° |
| <i>T.urogallus</i> , male | 4100 | 16.5 | 2.4 | 4.0 | 0.1 | 3.33 | 1364 | 1665 |
| <i>T.parvirostris</i> , male | 3040 | 18.5 | 2.0 | 2.5 | - | - | 955 | 989 |
| <i>T.parvirostris</i> , female | 1800 | 18.0 | 2.0 | 2.0 | - | - | 707 | 733 |
| <i>L.telrix</i> , male | 1200 | 15.6 | 4.25 | 4.1 | 0.05 | 1.25 | 689 | 733 |
| <i>L.lagopus</i> , male, female | 600 | 17.0 | 3.0 | 3.9 | 0.1 | 0.7 | 475 | 502 |
| <i>L.mutus</i> , male, female | 475 | 17.0 | 3.5 | 3.4 | 0.1 | - | 399 | 421 |
| <i>T.bonasia</i> , male, female | 400 | 19.5 | 1.5 | 3.0 | - | 0.5 | 360 | 376 |

T_n - night period, T_r - diurnal rest period, T_a - feeding activity period, T_{fl} - fly period.

perature keeping it at a comparatively stable level throughout all winter.

Mean temperatures in burrows are high enough to be close to the lower critical temperature in most species. Birds can keep burrow temperatures in limits between -5° to zero. It looks like the strongest question for a Grouse in the snow burrow is how to make the temperature lower. It's worth to note that the process of excretion also brings some energy for long-term staying under snow surface. Being formed in the rectal part of intestines, droppings partly loose water before wasting. After cooling in the burrow, some additional amount of energy emerges (for example, in the Hasel Grouse, Tetrastes bonasia, about 7 per cent of RM). In some cases this extra heat may likely be harmful. Meanwhile "liquid" coecal faeces are never waste before bird's coming off the snow.

The long history of the process of Grouses' adaptation to the life in snow burrows by indirect way is additionally confirmed by the fact that the lower critical temperature in many species is close just to the average level estimated in burrows.

The critical temperatures in Grouses are the lowest as compared with other bird species. It clearly accounts for well developed plumage and permanent process of digestion in the intestines, mostly in the coecal compartment. Thus, by using snow burrow Grouse birds actually used to spend long northern winters under temperatures conditions close to thermoneutrality.

SUMMARY

Daily energy budgets in 6 species of the family Tetraonidae, wintering in North Palaearctic at $T_a^{\circ} -20^{\circ} - -44^{\circ}$ were determined in two or three ways, including simultaneously measured time budget (Tabl.1).

The low level of winter's DEB is the result of: (1) low level of activity - the birds spend only 1-4 hours daily for obtaining the food; (2) the birds spend much time (20-23 hours daily) in snow burrows - the thermal refuges with constant T_a° of $-4^{\circ} - -5^{\circ}$; (3) the low lower critical T° . Using the thermal refuges, tetraonid birds may regulate average daily T_a° near -7° instead of $-10^{\circ} - -60^{\circ}$ in open air.

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DAILY BUDGETS OF TIME AND ENERGY IN WINTERING
LESSER WHITE-FRONTED GEESE ANSER ERYTHROPUS

T.D.Vorobyeva

Kyzyl-Agachski Preserve, USSR

Daily budgets of time and energy in lesser White-fronted Geese were studied during the period from November to March, 1978-1981, on the southwest coast of the Caspian Sea. Wintering flocks of up to ten thousand birds fed on barley (Hordeum vulgare) and rye grass (Lolium rigidum) in winter barley crops. The land activity was recorded by the method of Ebbinge et al. (1975), counting the number of birds concerned with each of the activities in a group of 100 to 500 birds. Time spent for short flights and for flying over to watering places and night shelters was recorded by direct observations. The night behavior was recorded twice by observations on moonlit nights. Altogether 18 daily time budgets were obtained (Table 1), with each of them, as it appears from the method, representing a mean statistical budget of several hundreds of birds.

The duration of the active period in lesser White-fronted Geese correlates with that of light day ($r=0.75$) and averages 10.79 ± 10 hr of which feeding accounts for 8.47 ± 0.23 hr.

The conversion of time budgets into daily energy budgets involved the use of the following coefficients (Dolnik, 1980): $1.0 \times \text{BM}$ (night rest), $1.12 \times \text{BM}$ (day rest), $1.3 \times \text{BN}$ (alertness, comfort movements, water drinking), $1.4 \times \text{BM}$ (feeding activity with walking), $6.0 \times \text{BM}$ (social conflicts), $12.0 \times \text{BM}$ (flight), $16 \times \text{BM}$ (take-off). Basal metabolism (21.06 kJ/hr) was computed on the basis of body weight ($1650-100 \text{ g}$, $n=8$) according to equation 5.5. (Ken-deigh, Dolnik, Gavrilov, 1977), and the energy value of thermoregulation ($9.42 \text{ kJ/}^\circ\text{C}$) by equations 5.25 and 5.31 of the same authors and by the environmental temperature which ranged from -1.0 up to 13.2°C .

T a b l e 1. Daily budgets of time (DTB) and energy (DEB) in lesser White-fronted Geese in Winter period

| Activities and indices | DTB, hr | DEB, kJ/d |
|---|------------------|------------------|
| Flight+flying up | 0.50 ± 0.05 | 125 ± 13.0 |
| Feeding activity | 8.47 ± 0.23 | 250.0 ± 6.7 |
| Walking | 0.10 ± 0.01 | 3.0 ± 0.2 |
| Alertness | 0.51 ± 0.04 | 14.1 ± 1.1 |
| Comfort movements | 0.30 ± 0.02 | 8.2 ± 0.7 |
| Social contacts | 0.02 ± 0.00 | 2.4 ± 0.4 |
| Water drinking | 0.09 ± 0.01 | 2.4 ± 0.2 |
| Day rest | 0.77 ± 0.09 | 18.3 ± 2.2 |
| Night rest | 13.24 ± 0.19 | 278.4 ± 4.1 |
| DEB _{30°} | | 702.1 ± 12.0 |
| Energy consumption for thermoregulation | | 218.1 ± 8.1 |
| DEB _{6.8°} | | 920.2 ± 14.9 |

The daily energy consumption thus computed for all types of activities (Table 1) averaged 702.12 ± 11.97 kJ/d and the energy consumption for thermoregulation 218.10 ± 8.08 kJ/d. The total DEB value (920.2 ± 14.9 kJ/d), when calculated by this method, is only 1.09 times higher than the DEB value (846.2 kJ/d) expected for non-sparrow birds according to equations 5.25 and 5.31 (Kendeigh et al., 1977) and mean environmental temperature 6.8°C . On some days DEB varied from 836.6 up to 1045.9 kJ/d.

According to the available data (Owen, 1972; Dorozynska, 1962; Winjgaarden, 1970; Marriott, Forbes, 1970; Ebbinge et al., 1975) in various species of geese the coefficient of food utilization MEC on a grass diet ranged from 0.22 to 0.40 averaging ca. 0.33. Using this MEC value and the measured diet's caloricity (19.13 kJ/g dry weight) it is possible to calculate that the daily food requirement of lesser White-fronted Geese amounts to 145.8 ± 2.4 g dry weight of greens cereals.

We measured the daily food requirement by comparing the reserves of forage plants on geese-isolated and open plots of pasture (Dinesman, Khodasheva, 1974; Ebbinge et al., 1975). Depending on the feeding conditions of the year at the beginning of the season, when the grass had not yet been grazed and affected by early frosts, the lesser White-fronted Geese consumed $105.9\text{--}140$ g of grass (dry weight) daily and in the second half of the season from 145.6 to 168.0 g. The daily consumption during the whole winter period averaged 146.4 ± 9.2 g ($n=6$). Taken the caloricities of grass and MEC indicated above, the results obtained according to this independent method show that DEB in the birds equals 924.3 ± 58.1 kJ/d, i.e. it matches the value derived by the first method.

The third independent method for evaluating DEB was that based on measuring the amount of faeces excreted by the bird (Ebbinge et al., 1975). It is known (Dorozynska, 1962) that the excretion of faeces in geese occurs at a constant rate. We found that the interval between defecations in lesser White-fronted Geese is 3.33 min, the dry weight of one excrement is 0.60 ± 0.01 , they have 26 defecation per night, in the morning the filling of the digestive tract takes 0.88 hr and the specific caloricity of faeces is 15.9 kJ/g dry weight. A daily portion of faeces ranged from 103.2 up to 132.0 g, averaging 118.1 ± 2.1 g ($n=18$). Taken the MEC indicated above, DEB according to this method equals 924.9 ± 16.4 kJ/d and food consumption 146.5 ± 2.6 g. Thus, the three independent methods gave very close results (Table 2).

T a b l e 2. Results of determination of some energy indices in lesser White-fronted Geese obtained by three independent methods

| Energy indices | Methods of determination | | |
|---------------------------------|--------------------------|----------------------|----------------------------|
| | by DTB | by daily food intake | by daily portion of faeces |
| DEB, kJ/d | 920.2 ± 14.9 | 924.2 ± 58.1 | 924.9 ± 16.4 |
| GE, kJ/d | 2788.5 ± 45.2 | 2800.6 ± 176.0 | 2802.7 ± 49.8 |
| EE, kJ/d | 1868.3 ± 30.3 | 1876.4 ± 116.9 | 146.5 ± 2.6 |
| Daily food intake, g dry weight | 145.8 ± 4 | 146.4 ± 9.2 | 146.5 ± 2.6 |

The energy of food, faeces and DEB measured independently make it possible to determine the food utilization coefficient twice: $MEC = DEB/GE = 920.2/2800.6 = 0.328$; $MEC = (GE - EE)/GE = (2800.5 - 1877.8)/2800.6 = 0.320$.

The literature on ornithology contains data on daily food portions for several species of geese (Owen, 1977). Recalculation of these data for a standard goose body weight of 1650 g (recalculation was made with regard for the fact that the food requirement changes proportionally to the mass of body raised to the power of 0.67) yields the following values: Anser anser - 144 g/d, A. brachyrhynchus - 129 g/d, Branta leucopsis - 132 g/d, B. bernicla - 141 g/d, which are very close to each other and to those obtained by us.

The daily consumption of grass during the season increased as indicated above, but the utilization coefficient decreased from 0.38 to 0.29. In November, the energy assimilated from food exceeded DEB by 14.5%; in December, the energy assimilated from food equaled DEB, and in January, February and March DEB exceeded the energy assimilated from food by 4.4%. The duration of feeding during winter varied from 7.27 ± 0.19 hr in November, 7.80 ± 0.54 hr in December to 8.7 ± 0.10 hr in January and 8.97 ± 0.34 hr in February.

The ratio of food-assimilated energy to daily energy expenditure for feeding indicates the efficiency of food procurement which at the beginning of the season was equal to 4.44 and at the end of the season 3.41. During the entire season this index in the lesser White-fronted Geese averaged 3.7. In another herbivorous species, Otis tetrax, in the same place and season it was equal to 3.8 (Vorobyeva, 1982). Long duration of feeding and its rather low efficiency in herbivorous birds contrast strikingly with the same indices in the wintering Tetraonidae which feed on branches, buds or coniferous needles: they spend 2-4 hours on feeding and show the efficiency of food procurement from 7.5 to 24.

Thus, the three independent methods for evaluating DEB yielded results closely coinciding with each other as well as with the DEB values calculated from time budgets in lesser White-fronted Geese. These values are well predicted on the basis of body weight, environmental temperature and equations of DEB dependence in non-sparrow birds on their body weight (Kendeigh et al., 1977).

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TIME AND ENERGY BUDGETS OF THE CHAFFINCH, FRINGILLA COELEBS,
DURING REPRODUCTIVE PERIOD AND PROBLEMS OF UNIVERSAL
COEFFICIENTS FOR THE CONVERTING TIME BUDGET TO ENERGY BUDGET

V.R.Dolnik, T.A.Ilyina

Zoological Institute of the USSR Academy of Sciences,
Leningrad, USSR

This paper is a short review of our modern publications in Russian. The detalizations of methods, species name and citations were given in our original publications.

The energy equivalents of most categories of activities and physiological variables were measured in the Chaffinch, Fringilla coelebs, during long period of extensive investigations (see Dolnik, 1982 a, b for review).

We (Ilyina, 1982) have compared daily energy budget (DEB) in daged Chaffinches during non-productive winter period and during early summer period by two methods simultaneously: (A) by conversion the daily time-activity budget (DTB) into DEB using these energy equivalents, and (B) by direct measurements of energy contents in daily food intake and daily excretion. The close concordance between data obtained by both methods (59.2 ± 0.6 kJ/day and 59.0 ± 1.34 kJ/day respectively in winter, or 73.3 ± 1.34 kJ/day and 71.5 ± 4.1 kJ/day in early summer respectively) shows that energy equivalents and procedure of conversion are adequate for this species.

In second series of experiments we have compared DTB and DEB in male Chaffinches in three conditions (in field, in small cages and in large aviary) during early summer. Daily energy expenditures (DEE) was examined also in cages and in aviary by method (B), and close concordance was found between data obtained by both methods for both rooms. In large aviary Chaffinches show most categories of free-living birds activities including flight. Therefore we assumed that our estimates of DEB of free-living birds are close to true value of DEE.

DEB in field (83 ± 2.2 kJ/day, including 73 kJ/day for self-maintenance and 10 kJ/day for reproductive behavior) was only 3% lower than DEB in aviary and only 9% higher than DEB of caged birds. However the compositions of DTB and DEB were very different in these three circumstances (Fig.1). In field birds spend equal time on pedal locomotions, short flits and flight. The first two activities which are necessary for feeding of this species, decrease in aviary. Both activities were replaced by increased spontaneous flight and by alert posture. In cage flight is impossible, and absent, but Chaffinches spend more time in spontaneous short flits and in spontaneous pedal locomotions. In aviary and in cage Chaffinch progressively compensated the reduction of energy expenditure for self-maintenance and for productive behavior by increase of the energy expenditure for spontaneous activities. We can conclude that species-specific DEE is not a simple sum of the necessary daily energy expenditures for maintenance and reproduction under a given environmental condition. Total DEE is a daily value of energy that is elected by natural selection and is enough for species-specific existence under moderate environmental conditions. Both free-living and caged birds are obliged to exhaust this amount of energy, a bird should correct its own DTB and DEB compo-

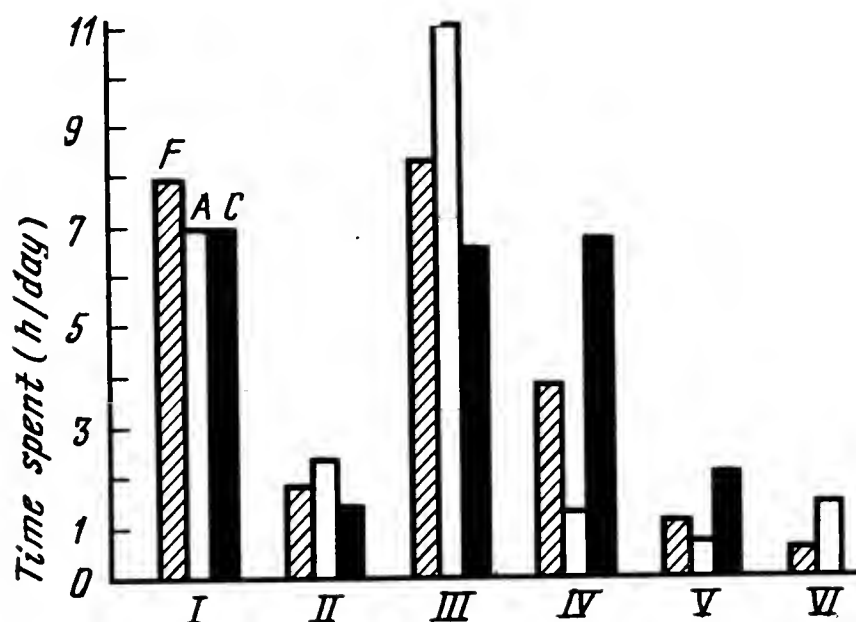
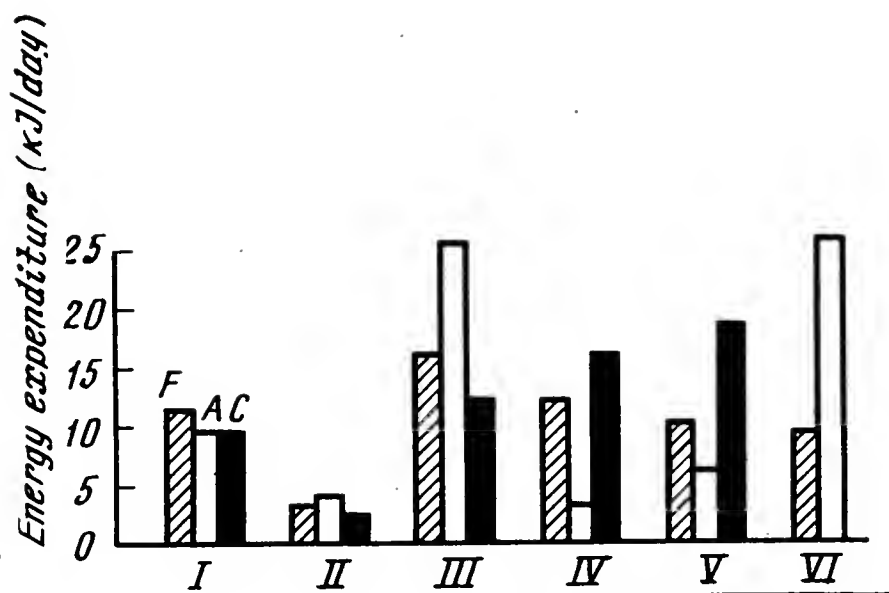


Fig. 1. Converting of DTB in DEB in male Chaffinches under three conditions: free-living (F), in large aviary (A), in cage (C). Six categories of activities and their energy costs are shown; nightly sleeping (I), daily resting (II), sitting alert (III), pedal locomotions (IV), short flights (V) and flight (VI)

situations for concordance between DEE and species-specific daily value of energy. The tendency to similarity of DEE between caged and free-living birds, or DEE during various seasons, or DEE between birds living in different parts of the area, is the result of this strategy.

We have compared data on DEE of free-living birds of 20 species with data on DEE of the same species under cage conditions. The differences were in range $\pm 10\%$ in 10 cases, and ratio between average DEE of free-living on the one hand and average DEE of caged birds on the other hand was 1:0.94 (Dolnik, 1982c; Dolnik, Kinzhevskaya, 1980).

The TAL method is the most effective of energy equivalents are measured for all categories of activities and for each species separately. However this situation is unreal. Another way is combination of data obtained with a few species in standard (infraspecies) system of equivalents. We have constructed the system of energy equivalents according to original measurements, revision of published data and some theoretical considerations (see Dolnik, 1980, 1982b,c). These standard (infraspecies) energy equivalents are

Fig. 2. Daily energy budgets of the free-living birds (circles and solid lines) in relation to ambient temperature, season and basal metabolic rate. Black circles are data on species during winter and non-reproductive seasons and open circles are data on species during reproductive seasons.

Upper panel: Estimations of the total daily energy budget according daily time budget of free-living birds and cost of thermoregulation in caged birds the same species or the same body mass.

Central panel: Daily energy budgets without cost of thermoregulation (DEB_{wct}) estimated according data on daily time budgets.

Lower panel: Estimation of the energy cost of thermoregulation in natural conditions obtained by extraction of DEB_{wct} from data on the daily energy expenditure (DEE) the same birds measured by another method.

To compare the data on energy cost of thermoregulation of every species they were divided by $m^{0.27}$, i.e. the slope of relation between body mass (m) and energy cost of thermoregulation in cage existence.

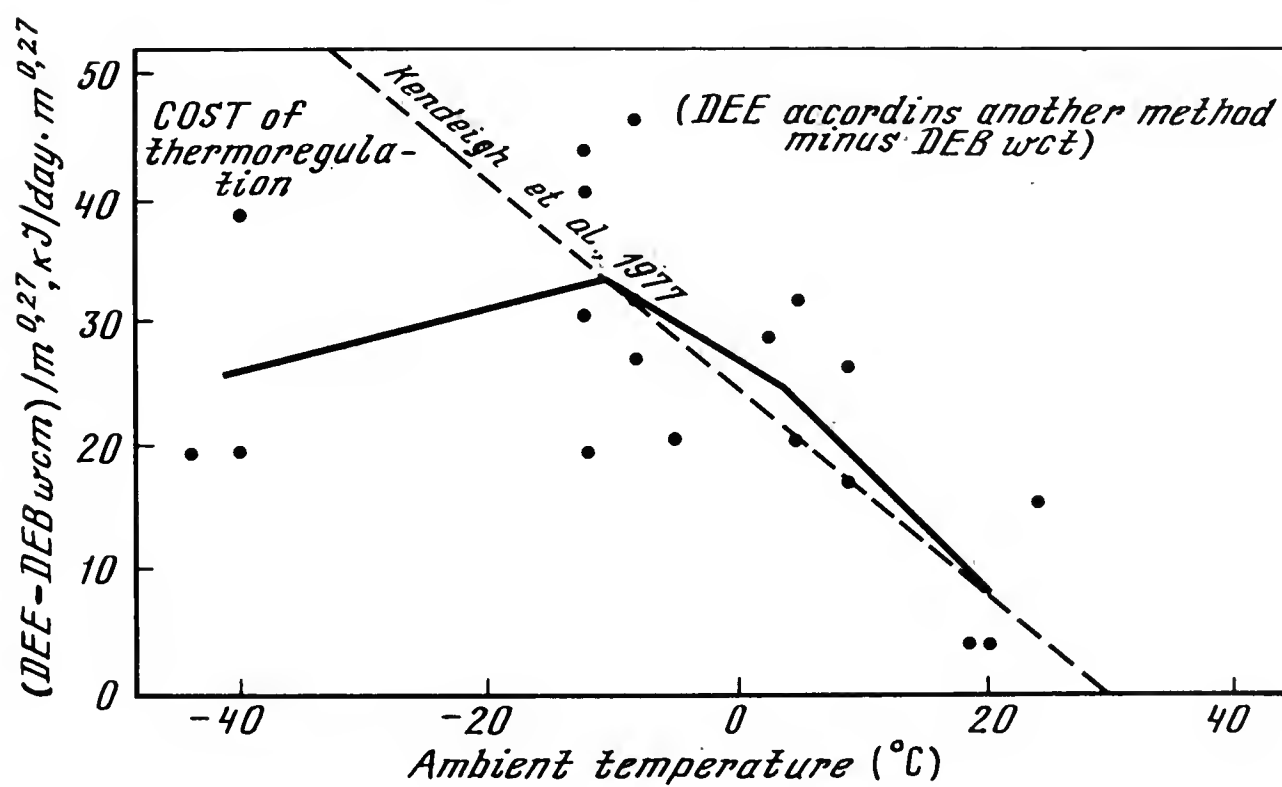
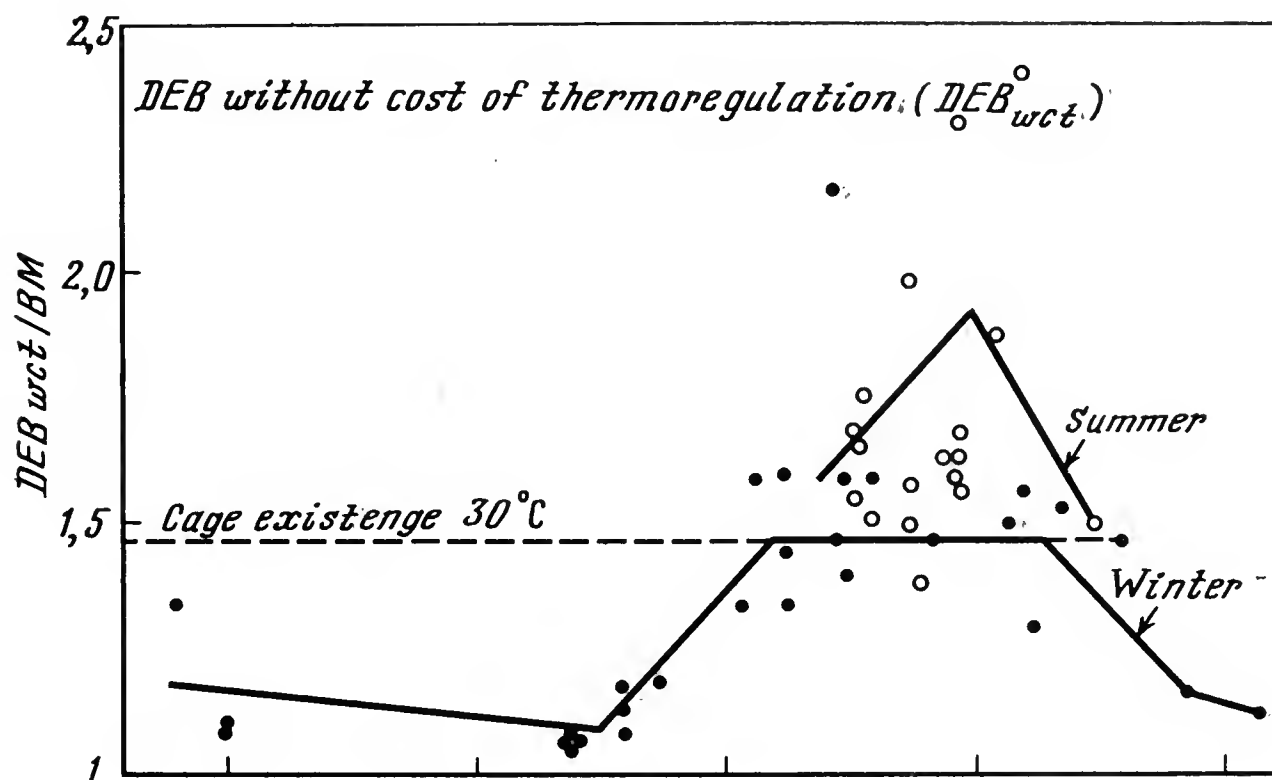
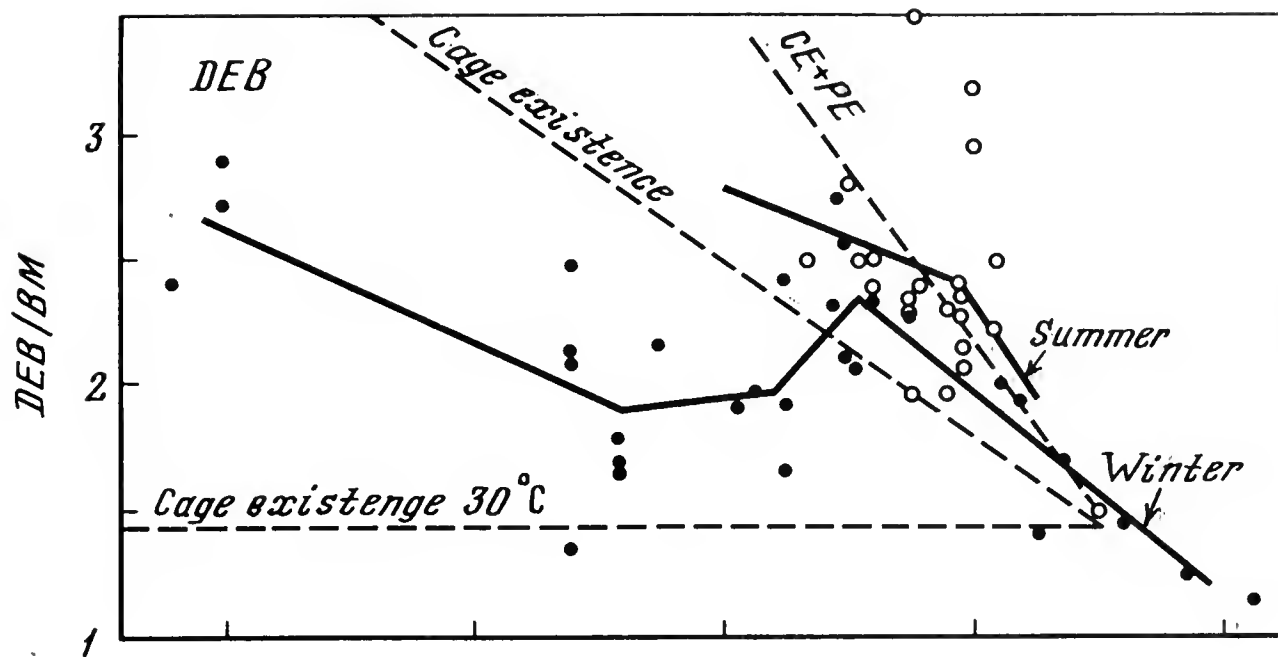
Interrupted lines show the cage existence energy at 30°C, cage existence energy in relation to ambient temperatures, cage existence energy plus productive energy (CE + PE) and energy cost of thermoregulation as they are predicted by Kendeigh et al., 1977 (equations)

(xBM): 1.0 for nightly sleeping, 1.12 for daily rest, 1.3 for alert posture, comfort behavior, eating, singing, feeding of youngs and all others activities without moving of body, 1.6 for all moderate pedal locomotions and soaring, 6.0 for all hard short-time non-flight activities and for flits, 16.0 for heavy flight. Cost of directional flight is $12 \cdot x \cdot BM$ in species which spend in flight up to 1 hour per day. For long-flying species the energy cost of flight (FC) is related to time spend in flight (t_f , h/day):

$$FC = 2.5 (\ln t_f \cdot 24^{-1} - 1) \cdot BM$$

Using standard equivalents, data on energy cost of thermoregulation in cage existence, basal metabolic rate (two last according to direct measurements or according to Kendeigh et al., 1977 equations) and standart procedure of calculation, we have estimated DEB for 39 bird species of 11 orders according published data on time-budgets of these species (see Dolnik, 1982 b, c, for explanations of the species name, data on DTB and references).

There are measurements of DEE by some separate methods for 20 of these 39 species. The $\pm 10\%$ concordance was found between calculated DEB and measured DEE in 16 species. The ratio between average DEB and average DEE was 1:1. This shows that a universal system of conversion of coefficients is possible. There were three reasons for this stability of energy costs of activities for many species. (1) The energy costs of most categories of activities (as times of BM) are similar in most species. (2) If a species is poorly adapted to given category of activity, this activity takes little of time and has slight effect on the daily energetic budget. (3) The depth of morphological and physiological adaptations of a species to one given cate-



gory of activity can reduce the adaptations to other categories of activities, and reduction of the energy cost of the given activity may be accompanied by slow increase of energy cost of other activities. As result can be reorganized the composition of DEB without change of total DEE. This illustrates the absence of correlation between species-specific DEE and species-specific time spent in flight (Dolnik, Kinzhevskaya, 1980; Dolnik, 1982 b, c).

The analysis of DEB of 39 species lead to several interesting conclusions about the DEB of free-living birds under usual for every species ambient temperatures (Fig.2): (1) 1.5 BM is an optimal level for DEB (without costs of thermoregulation and production). (2) 1.1 BM is the lowest level for DEB without costs of thermoregulation and production). Such level is known for some species under summer desert or winter subarctic climate. Under these conditions the competition is reduced and birds can reduce their activity and spend more time in roosting than in moderate climate. (3) 2.5 BM is an optimal level for DEB under moderate winter conditions and during productive season. (4) The shapes of the relation between ambient temperatures of the one hand and energy expenditures for activities, thermoregulation, production and DEE on the other hand are curvilinear, if we compare data on different species which live free under usual for them ambient conditions.

SUMMARY

There were several reasons for limitation of the range of DEE variations of birds: (1) adaptive reorganizations of the DTB and DEB structures in individual organism; (2) uniformity of energy cost of most similar categories of activities in most species; (3) reorganizations (during adaptive evolution) of energy cost of activities; (4) reduction of total activity, adaptive changes of insulative properties and increase of time spent in roosting in species which live in summer desert or winter subarctic conditions.

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BASAL METABOLIC RATE, THERMOREGULATION AND EXISTENCE
ENERGY IN BIRDS: WORLD DATA

V.M.Gavrilov, V.R.Dolnik

Department of Vertebrate Zoology, Moscow State University, Moscow, USSR;
Zoological Institute of the USSR Academy of Sciences, Leningrad, USSR

INTRODUCTION

The method of converting of time-budget data in free-living birds into energy-budget needs as minimum two experimental data obtained for birds: basal metabolic rate and thermal conductance. The conversion may be more accurately estimated when used additional information on thermoneutral zone and existence energy is used. There are three sources of information: (a) direct measurements on the same species, (b) calculation from allometric equations on the base of avian body mass and ambient temperature, and (c) published data on the same species.

The last one needs a condense publication of various experimental data dissipated in world literature. Reviews of Lasiewski, Dawson, 1967; Dawson, Hudson, 1970; Aschoff, Pohl, 1970; Whittow, 1976; Aschoff, 1981; Kendeigh et al., 1977, content a lot of data on energy metabolic rate in several species of birds. However all these authors select world data according to central aim of their works, and ignore some additional information (circadian cycle phase, season, ets.).

In present publication we collected world data on energy metabolism in various species of birds without selection, as complete, as possible. Some data are unrealistic, but the reader has a possibility of controlling them by comparison of experimental data with the values predicted by equation on the base of the body mass.

I. THERMOREGULATORY ENERGETICS IN BIRDS: WORLD DATA

Most measurements of heat production in birds under various ambient temperatures were fulfilled in standard conditions: birds were enclosed in darkness without locomotor activity and without heat increment of food. Energy expenditure in this conditions was named "standard metabolic rate" or "basal metabolic rate" or "resting metabolic rate". Energy expenditure in standard conditions varies with variations of ambient temperature in three different manners. Within thermoneutral zone it is independent from the ambient temperature variations. It increases inversely to the ambient temperature when this temperature is lower than the lower limit of the thermoneutral zone, and it increases with the elevation of the ambient temperature when the temperature is higher than the upper limit of the thermoneutral zone.

Three different terms are necessary for designation of these three branches of the "thermoregulatory curve". The term "basal metabolic rate" is used in this paper for designation of energy expenditure within thermoneutral zone. The term "standard metabolic rate" is used in this paper for nomination of the energy expenditure under ambient temperatures lower than the lower limit of the thermoneutral zone. The term "standard metabolic rate under heat stress" may designate the energy expenditure under the ambient temperatures higher than the upper limit of the thermoneutral zone.

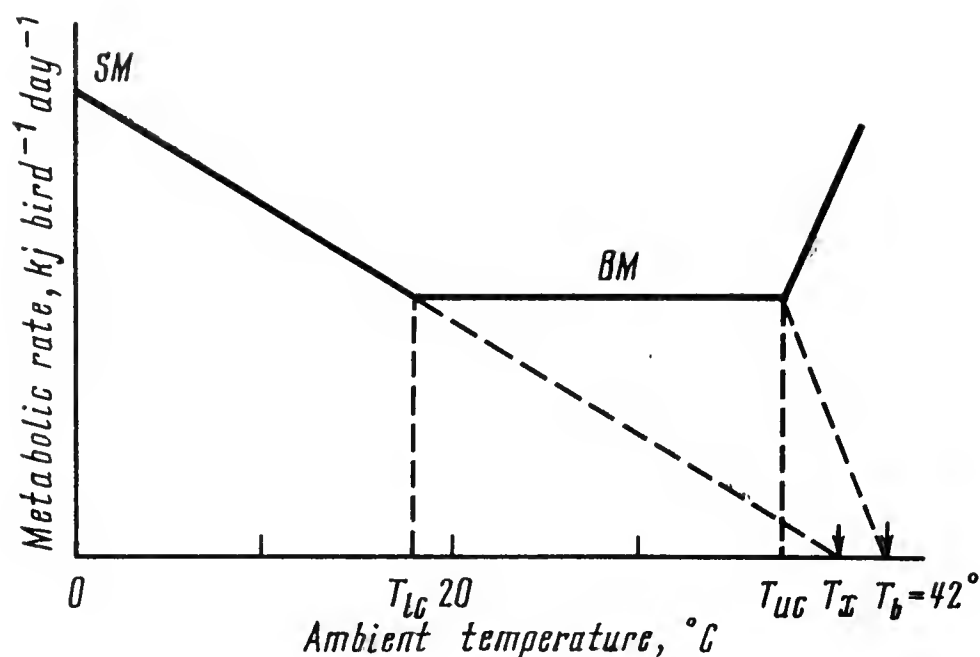


Fig. 1. Relation of energy expenditure on ambient temperature according Scholander's model and the main characteristics of energetic metabolism in rest. Denotations see text

Energy expenditures under standard conditions and variations of ambient temperature may be described according to the Scholander model by several indices (Fig. 1):

T_a = ambient temperature ($^{\circ}\text{C}$),

T_b = body temperature ($^{\circ}\text{C}$),

T_x = the "body temperature" extrapolation after the linear regression of the standard metabolic rate ($^{\circ}\text{C}$) and equivalent to the value of T_a at $\text{SM} = 0$,

T_{lc} = lower critical temperature ($^{\circ}\text{C}$) of the thermoneutral zone,

T_{uc} = upper critical temperature ($^{\circ}\text{C}$) of the thermoneutral zone,

BM = basal metabolic rate ($\text{kJ bird}^{-1} \text{ day}^{-1}$) within thermoneutral zone,

SM_0 = standard metabolic rate ($\text{kJ bird}^{-1} \text{ day}^{-1}$) under the ambient temperature 0°C , as it is predicted by the linear regression of SM on T_a ,

h_l = thermal conductance or heat transfer coefficient ($\text{kJ bird}^{-1} \text{ day}^{-1} \text{ }^{\circ}\text{C}^{-1}$) at $T_a = T_{lc}$,

h_u = thermal conductance or heat transfer coefficient ($\text{kJ bird}^{-1} \text{ day}^{-1} \text{ }^{\circ}\text{C}^{-1}$) at $T_a = T_{uc}$. It is the highest value of the thermal conductance in birds without additional energy expenditure for increasing of heat dissipation.

In Table 1 presented below world data on BM , SM_0 , h_l , h_u , T_{lc} and T_{uc} are summarized for 193 non-passerines and 260 passerines avian species. This collection of data is several times more than that published earlier by Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970; Dawson and Hudson, 1970; Kendeigh et al., 1977; in relation to BM ; it is 2-8 times more than the collection by Lasiewski et al., 1967; Kendeigh et al., 1977; Aschoff, 1981 in relation to h_l : it is 2 times more than the collection by Kendeigh et al., 1977, in relation to T_{lc} , and this collection is the first in relation to h_u and T_{uc} .

Table 1. Thermoregulatory energetics in birds

| Species | Body mass, g | Season | Time of measurements | SM, $\text{kJ bird}^{-1} \text{day}^{-1}$ | h_1 $\text{kJ bird}^{-1} \text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$ | h_2 $\text{kJ bird}^{-1} \text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$ | Critical temperatures | | BM $\text{kJ bird}^{-1} \text{day}^{-1}$ | References |
|------------------------|--------------|--------|----------------------|---|--|--|------------------------|------------------------|--|-------------------------|
| | | | | | | | Lower $^\circ\text{C}$ | Upper $^\circ\text{C}$ | | |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 8 | 10 | 11 |
| <u>Sphenisciformes</u> | | | | | | | | | | |
| Eudyptes cristatus | 2330 | W | N | 764.5 | 16.25 | 50.45 | 16.0 | 32.0 | 504.5 | Gavrilov, 1977 |
| Spheniscus humboldti | 3870 | ? | (N) | 1327.3 | (77.94) | 48.28 | 6.5 | 25.0 | 820.7 | Drent, Stonehouse, 1971 |
| Eudyptes chrysolophus | 3870 | W | N | 1296.2 | 44.03 | 62.30 | 12.0 | 30.0 | 747.8 | Gavrilov, 1977 |
| Aptenodytes patagonica | 11080 | W | N | 2100.2 | 70.34 | 134.95 | 3.0 | 28.0 | 1899.2 | Gavrilov, 1977 |
| Aptenodytes forsteri | 23370 | S | D | 884.0 | 75.52 | 52.00 | -10.0 | 25.0 | 884.0 | Pinshow et al., 1976 |
| Aptenodytes forsteri | 25090 | W | D | 1001.3 | 122.60 | 58.9 | -10.0 | 25.0 | 1001.3 | Le Maho et al., 1976 |
| <u>Pelecaniformes</u> | | | | | | | | | | |
| Anhinga anhinga | 1040 | S | N | 568.09 | 18.26 | | 26.0 | | 275.9 | Henneman, 1983 |
| Anhinga anhinga | 1040 | S | D | 972.92 | 22.78 | | 29.5 | | 301.0 | Henneman, 1983 |
| Phalacrocorax auritus | 1330 | S | N | 834.1 | 20.53 | | 17.5 | | 474.8 | Henneman, 1983 |
| Phalacrocorax auritus | 1330 | S | D | 1041.1 | 23.61 | | 21.0 | | 545.3 | Henneman, 1983 |
| <u>Ciconiiformes</u> | | | | | | | | | | |
| Florida coerulea | 290.3 | S | D | 286.3 | 7.25 | | 27.5 | | 86.8 | Ellis, 1980 |
| Bubulcus ibis | 298.7 | S | D | 328.2 | 7.72 | | 27.6 | | 115.0 | Ellis, 1980 |
| Hydranassa tricolor | 309.9 | S | D | 377.0 | 8.91 | | 25.8 | | 147.1 | Ellis, 1980 |
| Egretta thula | 313.9 | S | D | 323.0 | 7.80 | | 26.2 | | 118.7 | Ellis, 1980 |
| <u>Anseriformes</u> | | | | | | | | | | |
| Aix sponsa | 448 | S | N | 352.1 | 8.70 | 32.10 | 18.0 | 36.0 | 194.3 | Gavrilov, 1980, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|-------------------------|------|---|---|---------|-------|-------|------|------|--------|---------------------------------|
| Aix sponsa | 448 | S | D | 390.9 | 10.60 | | 16.0 | 35.0 | 221.5 | Gavrillov, 1985 |
| Aix sponsa | 468 | W | N | 357.1 | 8.42 | 34.26 | 17.0 | 36.0 | 205.6 | Gavrillov, 1981 |
| Aix sponsa | 468 | W | D | 402.8 | 10.78 | | 12.0 | 34.0 | 273.4 | Gavrillov, 1981 |
| Anas penelope | 723 | S | N | 404.9 | 10.05 | | 16.0 | | 244.1 | Gavrillov, 1980, 1982 |
| Anas penelope | 718 | W | N | 371.0 | 9.20 | | 12.1 | | 260.4 | Gavrillov, 1980, 1982 |
| Anas rubripes | 904 | W | D | 522.5 | 11.26 | | 19.0 | | 308.6 | Hartung, 1967 |
| Anas platyrhynchos | 1020 | S | N | 535.9 | 13.16 | 70.34 | 14.0 | 37.0 | 351.7 | Gavrillov, 1980, 1982 |
| Anas platyrhynchos | 1020 | S | D | 611.0 | 16.28 | / | 12.0 | 36.0 | 415.6 | Gavrillov, 1985 |
| Anas platyrhynchos | 1132 | W | N | 544.3 | 13.61 | 72.67 | 8.0 | 36.0 | 435.4 | Gavrillov, 1981 |
| Anas platyrhynchos | 1132 | W | D | 610.9 | 14.65 | | 3.0 | 34.0 | 566.9 | Gavrillov, 1981 |
| Anas platyrhynchos | 1263 | W | D | 766.6 | 14.95 | | 22.0 | | 438.0 | Hartung, 1967 |
| Anas platyrhynchos ♀ | 1084 | W | D | 930.8 | 27.19 | | 20.0 | | 386.9 | Smith, Prince, 1973 |
| Anas platyrhynchos ♂ | 1248 | W | D | 1185.8 | 32.51 | | 20.0 | | 535.5 | Smith, Prince, 1973 |
| Anser anser | 3250 | S | N | 1440.7 | 35.92 | 93.79 | 14.0 | 32.0 | 937.9 | Gavrillov, Dolnik (unpublished) |
| Cygnus olor | 8300 | S | ? | 2662.6 | 56.05 | 96.99 | 0.8 | 15.0 | 2618.6 | Bech, 1980 |
| Cygnus olor | 8914 | W | ? | 4003.4 | 30.10 | | 5.5 | | 3837.9 | Bech, 1980 |
| <u>Falconiformes</u> | | | | | | | | | | |
| Falco tinnunculus | 131 | A | N | 139.4 | 3.62 | 11.17 | 20.0 | 36.0 | 67.0 | Gavrillov (unpublished) |
| Accipiter nisus | 135 | S | N | 164.1 | 4.32 | 13.68 | 19.0 | 36.0 | 82.1 | Gavrillov, Dolnik (unpublished) |
| Falco subbuteo | 208 | A | N | 224.4 | 5.61 | 18.70 | 20.0 | 35.0 | 112.2 | Gavrillov, Dolnik (unpublished) |
| Pernis apivorus | 652 | S | N | 400.3 | 9.90 | 25.28 | 20.0 | 34.0 | 202.2 | Gavrillov, Dolnik (unpublished) |
| Coragyps atratus | 2120 | ? | D | (818.3) | 10.24 | | 25.0 | 40.0 | 562.3 | Larochelle et al., 1982 |
| <u>Galliformes</u> | | | | | | | | | | |
| Excalfactoria chinensis | 44 | S | N | 77.0 | 2.00 | 8.78 | 21.0 | 38.0 | 35.15 | Gavrillov, 1985 |
| Excalfactoria chinensis | 44 | S | D | 78.6 | 2.39 | | 18.0 | 35.0 | 35.56 | Gavrillov, 1985 |
| Excalfactoria chinensis | 41 | W | N | 94.6 | 2.32 | 12.67 | 19.0 | 38.0 | 50.7 | Gavrillov, 1981 |
| Excalfactoria chinensis | 41 | W | D | 100.5 | 2.23 | | 18.0 | 37.0 | 60.3 | Gavrillov, 1981 |
| Coturnix coturnix | 97 | S | N | 154.1 | 3.85 | 19.26 | 20.0 | 38.0 | 77.0 | Gavrillov, 1980, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|------------------------|------|----|---|--------|-------|--------|------|------|--------|------------------------------------|
| Coturnix coturnix | 97 | S | D | 151.0 | 3.57 | | 19.0 | 36.0 | 83.2 | Gavrilov, 1985 |
| Coturnix coturnix | 109 | W | N | 136.9 | 3.44 | 17.9 | 19.0 | 38.0 | 71.6 | Gavrilov, 1981 |
| Coturnix coturnix | 109 | W | D | 148.6 | 3.51 | | 18.0 | 37.0 | 85.4 | Gavrilov, 1981 |
| Lophortix californicus | 138 | SW | ? | 185.9 | 4.50 | 14.61 | 27.3 | 37.5 | 65.7 | Brush, 1965 |
| Lagopus leucurus | 326 | S | N | 251.6 | 7.39 | 51.08 | 6.5 | 38.0 | 204.3 | Johnson, 1968 |
| Lagopus mutus | 432 | W | D | 287.6 | 7.47 | | 1.3 | | 325.7 | West, 1972 |
| Perdix perdix | 483 | S | N | 373.9 | 9.26 | 51.81 | 18.0 | 38.0 | 207.3 | Gavrilov, 1980, 1982 |
| Perdix perdix | 483 | S | D | 411.3 | 11.59 | | 16.0 | 36.0 | 225.9 | Gavrilov, 1985 |
| Perdix perdix | 501 | W | N | 298.1 | 7.83 | 37.26 | 15.0 | 37.0 | 186.3 | Gavrilov, 1981 |
| Perdix perdix | 501 | W | D | 356.7 | 8.09 | | 15.0 | 35.0 | 235.3 | Gavrilov, 1981 |
| Lagopus lagopus | 524 | S | N | 410.7 | 10.27 | 67.20 | 14.0 | 38.0 | 268.8 | Gavrilov, 1980, 1982 |
| Lagopus lagopus | 524 | S | D | 455.9 | 12.26 | | 12.0 | 35.0 | 306.4 | Gavrilov, 1985 |
| Lagopus lagopus | 567 | W | N | 330.3 | 8.21 | 49.66 | 10.0 | 37.0 | 248.3 | Gavrilov, 1981 |
| Lagopus lagopus | 567 | W | D | 392.7 | 10.71 | | 6.0 | 35.0 | 328.7 | Gavrilov, 1981 |
| Lagopus lagopus | 539 | S | N | 407.0 | 10.60 | | 7.7 | | 329.9 | West, 1972 |
| Lagopus lagopus | 590 | W | D | 257.5 | 6.40 | | 6.3 | | 295.2 | West, 1972 |
| Alectoris graeca | 620 | S | N | 425.4 | 10.56 | 49.32 | 17.0 | 37.0 | 246.6 | Gavrilov, 1980, 1982 |
| Alectoris graeca | 633 | W | N | 335.8 | 8.34 | 43.80 | 14.0 | 37.0 | 219.0 | Gavrilov, 1980, 1982 |
| Alectoris graeca | 647 | ? | ? | 440.6 | 8.10 | 22.01 | 24.5 | 31.0 | 242.1 | Laudenslager, Hammel, 1978 |
| Bonasa umbellus | 644 | W | N | 205.2 | 3.73 | | 0.3 | | 206.0 | Rasmussen, Brander, 1973 |
| Domestic fowl | 2430 | ? | D | 811.4 | 8.16 | | 18.3 | | 671.6 | Barott, Pringle, 1946 |
| Tetrao urogallus ♀ | 3900 | S | N | 1373.3 | 34.3 | 206.00 | 10.0 | 37.0 | 1030.0 | Gavrilov, 1980, 1982 |
| Tetrao urogallus ♀ | 4010 | W | N | 1130.5 | 27.21 | 170.27 | 4.0 | 36.0 | 1021.6 | Gavrilov, 1980, 1982 |
| <u>Gruiformes</u> | | | | | | | | | | |
| Crex crex | 96 | S | N | 151.1 | 3.77 | 17.06 | 22.0 | 38.0 | 68.2 | Gavrilov, Dolnik (unpubplished) |
| Fulica atra | 412 | S | N | 290.6 | 7.14 | 29.38 | 16.0 | 36.0 | 176.3 | Gavrilov, 1980, 1982 |
| Fulica atra | 436 | W | N | 313.2 | 7.74 | 34.05 | 14.0 | 36.0 | 204.3 | Gavrilov, 1980, 1982 |
| Fulica atra | 780 | W | N | 422.0 | 14.24 | | 13.0 | | 241.2 | J.Mertens (personal communication) |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---------------------------|-------|---|---|-------|-------|-------|------|--------|-------|--|
| <u>Charadriiformes</u> | | | | | | | | | | |
| Charadrius dubius | 36 | S | N | 80.0 | 2.00 | 9.00 | 22.0 | 38.0 | 36.0 | Gavrilov, 1980, 1982 |
| Charadrius dubius | 44 | W | N | 82.1 | 2.13 | 10.36 | 19.0 | 38.0 | 41.5 | Gavrilov, 1980, 1982 |
| Sterna fuscata | 150.4 | S | D | 199.5 | 5.16 | 10.05 | 25.0 | 35.0 | 70.4 | MacMillen et al., 1977 |
| Larus ridibundus | 253 | S | D | 294.8 | 5.24 | | (20) | | 190.0 | Davydov, 1971 |
| Larus ridibundus | 290 | W | D | 270.1 | 4.76 | | (18) | | 184.5 | Davydov, 1971 |
| Larus ridibundus | 285 | S | N | 290.2 | 7.30 | 57.78 | 16.0 | 39.0 | 173.3 | Gavrilov, 1980, 1982 |
| Larus ridibundus | 285 | S | D | 301.6 | 7.68 | | 14.0 | 37.0 | 194.1 | Gavrilov, 195 |
| Larus ridibundus | 306 | W | N | 256.2 | 6.36 | 40.20 | 15.0 | 38.0 | 160.8 | Gavrilov, 1981 |
| Larus ridibundus | 306 | W | D | 271.3 | 6.02 | | 13.0 | 36.0 | 193.0 | Gavrilov, 1981 |
| Larus canus | 428 | S | N | 345.0 | 9.60 | 50.24 | 15.0 | 38.0 | 201.0 | Gavrilov, 1980, 1982 |
| Larus canus | 428 | S | D | 355.4 | 10.02 | | 14.0 | 35.0 | 215.0 | Gavrilov, 1985 |
| Larus canus | 431 | W | N | 296.2 | 7.86 | 48.58 | 13.0 | 38.0 | 194.3 | Gavrilov, 1981 |
| Larus canus | 431 | W | D | 316.5 | 7.26 | | 9.0 | 36.0 | 251.2 | Gavrilov, 1981 |
| Scolopax rusticola | 430 | S | N | 339.6 | 8.91 | 37.35 | 18.0 | 37.0 | 186.7 | Gavrilov, 1981b |
| <u>Columbiformes</u> | | | | | | | | | | |
| Lophophaps ferruginea | 81 | S | N | 125.2 | 2.81 | 11.44 | 33.0 | 39.0 | 34.3 | Dawson, Bennett, 1973 |
| Lenidura macroura | 91 | ? | N | 189.2 | 4.44 | 12.48 | 30.0 | 37.5 | 56.1 | Hudson, Brush, 1964 |
| Streptopelia senegalensis | 108 | S | N | 162.9 | 4.07 | 18.32 | 22.0 | 38.0 | 73.3 | Gavrilov, Dolnik (unpublished) |
| Streptopelia turtur | 154 | A | N | 219.0 | 5.48 | 24.60 | 22.0 | 38.0 | 98.4 | Gavrilov, Dolnik (unpublished) |
| Streptopelia decaocto | 187 | W | N | 192.6 | 4.25 | | 19.5 | | 110.1 | J.A.L.Mertens (personal communication) |
| Columba livia | 314 | W | D | 268.4 | 6.36 | | 19.0 | 29.0 | 145.7 | Kayser, 1940 |
| Columba livia | 315 | ? | N | 244.1 | 3.94 | 27.33 | 23.0 | 36.5 | 150.3 | Calder, Schmidt-Nielsen, 1967 |
| Columba livia | 353 | W | N | 276.8 | 6.85 | 40.10 | 17.0 | (38.0) | 160.4 | Gavrilov, 1981 |
| Columba livia | 353 | W | D | 291.4 | 7.04 | | 16.0 | 35.0 | 178.8 | Gavrilov, 1981 |
| Columba livia | 368 | S | N | 252.8 | 4.76 | 47.73 | 23.0 | 39.0 | 143.2 | Gavrilov, 1985 |
| Columba livia | 368 | S | D | 281.4 | 6.35 | | 20 | 38.0 | 154.4 | Gavrilov, 1985 |
| Columba palumbus | 493 | A | N | 340.4 | 8.05 | 42.82 | 21.0 | 38.0 | 171.3 | Gavrilov, Dolnik (unpublished) |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--------------------------------|-------|---|-----|-------|-------|--------|------|------|-------|--------------------------------|
| <u>Psittaciformes</u> | | | | | | | | | | |
| <i>Melopsittacus undulatus</i> | 25.2 | S | N | 80.0 | 2.00 | 8.65 | 27.0 | 39.0 | 26.0 | Gavrilov, 1980, 1982 |
| <i>Melopsittacus undulatus</i> | 25.2 | S | D | 81.6 | 2.14 | | 25.0 | 38.0 | 28.0 | Gavrilov, 1985 |
| <i>Melopsittacus undulatus</i> | 33.6 | W | N | 76.2 | 1.83 | 8.13 | 26.0 | 38.5 | 28.5 | Gavrilov, 1981 |
| <i>Melopsittacus undulatus</i> | 33.6 | W | D | 79.5 | 2.00 | | 24 | 37.5 | 31.4 | Gavrilov, 1981 |
| <i>Melopsittacus undulatus</i> | 33.7 | W | N | 91.8 | 2.06 | (31.9) | 29.0 | 41.0 | 31.9 | Weathers, Schoenbaeher, 1976 |
| <i>Agapornis roseicollis</i> | 48.1 | S | N | 114.7 | 2.87 | 13.40 | 26.0 | 39.0 | 40.2 | Gavrilov, 1980, 1982 |
| <i>Agapornis roseicollis</i> | 48.1 | S | D | 117.0 | 3.04 | | 24.0 | 38.0 | 44.0 | Gavrilov, 1985 |
| <i>Agapornis roseicollis</i> | 48.4 | W | N | 113.9 | 2.83 | 13.40 | 25.0 | 39.0 | 40.2 | Gavrilov, 1981 |
| <i>Agapornis roseicollis</i> | 48.4 | W | D | 150.7 | 4.24 | | 26.0 | 37.0 | 53.2 | Gavrilov, 1981 |
| <i>Bolborhynchus lineola</i> | 54.5 | S | N | 153.0 | 3.63 | | 28.0 | 30.0 | 51.0 | Bucher, 1981 |
| <i>Agapornis fisheri</i> | 56.7 | W | N | 117.7 | 2.88 | 11.41 | 25.0 | 38.0 | 45.6 | Gavrilov, Dolnik (unpublished) |
| <i>Myiopsitta monachus</i> | 80.4 | W | D | 161.3 | 3.92 | 18.63 | 24.5 | 38.5 | 65.2 | Weathers, Caccamise, 1975 |
| <i>Myiopsitta monachus</i> | 83.1 | S | D | 181.2 | 4.04 | 34.05 | 28.0 | 40.0 | 68.1 | Weathers, Caccamise, 1978 |
| <i>Myiopsitta monachus</i> | 81.5 | ? | ? | 161.2 | 3.73 | 33.91 | 25.0 | 40.0 | 67.8 | Caccamise et al., 1974 |
| <i>Nymphicus hollandicus</i> | 85.6 | S | N | 149.9 | 3.77 | 19.83 | 24.0 | 39.0 | 59.5 | Gavrilov, 1980, 1982 |
| <i>Nymphicus hollandicus</i> | 85.6 | S | D | 154.4 | 3.71 | | 24.0 | 37.0 | 65.4 | Gavrilov, 1985 |
| <i>Nymphicus hollandicus</i> | 94.3 | W | N | 164.5 | 4.09 | 24.84 | 22.0 | 39.0 | 74.5 | Gavrilov, 1981 |
| <i>Nymphicus hollandicus</i> | 94.3 | W | D | 172.9 | 4.23 | | 20.0 | 37.0 | 88.3 | Gavrilov, 1981 |
| <u>Cuculiformes</u> | | | | | | | | | | |
| <i>Cuculus canorus</i> | 111.6 | S | N | 161.2 | 4.04 | 18.11 | 22.0 | 38.0 | 72.4 | Gavrilov, Dolnik (unpublished) |
| <i>Geococcyx californianus</i> | 284.7 | ? | N | 239.1 | 4.11 | 21.07 | 27.0 | 36.0 | 126.4 | Calder, Schmidt-Nielsen, 1967 |
| <u>Strigiformes</u> | | | | | | | | | | |
| <i>Micrathene whitneyi</i> | 45.9 | ? | W | 64.1 | 1.33 | 5.55 | 27.0 | 38.0 | 22.19 | Ligon, 1968, 1969 |
| <i>Speotyto cunicularia</i> | 132.4 | S | D | 157.8 | 3.64 | 13.40 | 25.0 | 37.0 | 67.0 | Coulombe, 1970 |
| <i>Speotyto cunicularia</i> | 142.7 | W | D | 112.2 | 2.14 | 11.72 | 25.0 | 37.0 | 58.6 | Coulombe, 1970 |
| <i>Asio otus</i> | 236 | S | N | 205.6 | 5.14 | 22.61 | 18.0 | 37.0 | 113.0 | Gavrilov, Dolnik (unpublished) |
| <i>Nyctea scandiaca</i> | 2024 | W | D,N | 412.0 | 11.47 | | 4.2 | | 364.3 | Gessaman, 1972 |

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|--------------------------|------|---|----------------|-------|---------|---------|------|------|------|--------------------------------|
| <u>Caprimulgiformes</u> | | | | | | | | | | |
| Phalaenoptilus nuttali | 40 | ? | ? | 78.3 | 1.80 | (15.49) | 35.0 | 44.0 | 15.5 | Bartholomew et al., 1962 |
| Chordeilus minor | 72 | ? | D | 131.9 | 3.47 | | 27.0 | | 38.1 | Lasiewski, Dawson, 1964 |
| Caprimulgus europaeus | 77.4 | S | N | 123.9 | 3.10 | | 22.0 | 38.0 | 55.7 | Gavrilov, Dolnik (unpublished) |
| Podargus ocellatus | 145 | S | D | 139.8 | 3.07 | (49.0) | 30.0 | 43.0 | 49.0 | Lasiewski et al., 1970 |
| <u>Apodiformes</u> | | | | | | | | | | |
| Ocreatus underwoodii | 2.7 | ? | N | 31.1 | 0.75 | | | | | Krüger et al., 1982 |
| Ocreatus underwoodii | 2.7 | ? | D | 54.9 | 0.99 | | | | | Krüger et al., 1982 |
| Ocreatus underwoodii | 2.7 | ? | N _t | 4.6 | 0.09 | | | | | Krüger et al., 1982 |
| Chlorostilbon mellisugus | 2.9 | ? | N | 22.1 | 0.38 | | | | | Krüger et al., 1982 |
| Chlorostilbon mellisugus | 2.9 | ? | D | 55.1 | 0.95 | | | | | Krüger et al., 1982 |
| Chlorostilbon mellisugus | 2.9 | ? | N _t | 7.7 | 0.28 | | | | | Krüger et al., 1982 |
| Orthorhynchus cristatus | 2.9 | ? | N | 17.7 | 0.22 | | | | | Krüger et al., 1982 |
| Orthorhynchus cristatus | 2.9 | ? | D | 34.2 | 0.24 | | | | | Krüger et al., 1982 |
| Orthorhynchus cristatus | 2.9 | ? | N _t | 6.1 | 0.13 | | | | | Krüger et al., 1982 |
| Orthorhynchus cristatus | 2.9 | ? | N | 28.4 | 0.79 | | | | | Krüger et al., 1982 |
| Orthorhynchus cristatus | 2.9 | ? | D | 44.1 | 0.94 | | | | | Krüger et al., 1982 |
| Orthorhynchus cristatus | 2.9 | ? | N _t | 6.9 | 1.46 | | | | | Krüger et al., 1982 |
| Archilochus alexandri | 2.9 | ? | N | 23.1 | -0.20 | | | | | Krüger et al., 1982 |
| Archilochus alexandri | 2.9 | ? | D | 42.1 | 0.23 | | | | | Krüger et al., 1982 |
| Archilochus alexandri | 3.2 | ? | N | 33.1 | 0.82 | | | | | Krüger et al., 1982 |
| Archilochus alexandri | 3.2 | ? | D | 49.0 | 0.63 | | | | | Krüger et al., 1982 |
| Archilochus alexandri | 3.3 | ? | N, D | 22.6 | 0.59 | | 28.5 | | 5.4 | Lasiewski, 1963 |
| Calypte costae | 3.2 | ? | D | 28.9 | 0.85 | 1.54 | 28.5 | 39.0 | 4.6 | Lasiewski, 1963 |
| Acestrura mulsant | 3.3 | ? | N | 16.2 | 0.10 | | | | | Krüger et al., 1982 |
| Acestrura mulsant | 3.3 | ? | D | 43.3 | 0.40 | | | | | Krüger et al., 1982 |
| Acestrura mulsant | 3.3 | ? | N _t | 2.2 | (+0.02) | | | | | Krüger et al., 1982 |

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|----------------------------|-----|---|----------------|------|----------|------|------|------|------|----------------------------|
| Selasphorus sassin | 3.7 | ? | D | 35.6 | 1.02 | | 28.5 | | 5.9 | Lasiewski, 1963 |
| Urosticte benjamini | 3.9 | ? | N | 35.3 | 0.92 | | | | | Krüger et al., 1982 |
| Urosticte benjamini | 3.9 | ? | D | 76.2 | 1.96 | | | | | Krüger et al., 1982 |
| Selasphorus rufus | 3.8 | ? | D | 30.1 | 0.84 | | 28.5 | | 5.9 | Lasiewski, 1963 |
| Trochilus seitulus | 4.0 | ? | N | 16.4 | (+0.34) | | | | | Krüger et al., 1982 |
| Trochilus seitulus | 4.0 | ? | D | 39.8 | (+0.47) | | | | | Krüger et al., 1982 |
| Trochilus seitulus | 4.0 | ? | N _t | 6.0 | (+0.002) | | | | | Krüger et al., 1982 |
| Calypte anna | 4.8 | ? | D | 38.1 | 1.02 | | 28.5 | | 10.0 | Lasiewski, 1963 |
| Chrysuronia oenone | 5.0 | ? | N | 33.6 | 0.24 | | | | | Krüger et al., 1982 |
| Chrysuronia oenone | 5.0 | ? | D | 62.9 | 0.34 | | | | | Krüger et al., 1982 |
| Chrysuronia oenone | 5.0 | ? | N _t | 5.0 | (+0.14) | | | | | Krüger et al., 1982 |
| Eugenes fulgens | 6.6 | ? | D | 38.1 | 0.95 | | 31.0 | | 8.8 | Lasiewski, Lasiewski, 1967 |
| Eugenes fulgens | 7.9 | ? | N | 50.2 | 0.89 | | | | | Krüger et al., 1982 |
| Eugenes fulgens | 7.9 | ? | D | 97.8 | 1.65 | | | | | Krüger et al., 1982 |
| Eugenes fulgens | 7.9 | ? | N _t | 12.5 | 0.04 | | | | | Krüger et al., 1982 |
| Florisuga mellivora | 6.9 | ? | N | 37.1 | 0.10 | | | | | Krüger et al., 1982 |
| Florisuga mellivora | 6.9 | ? | D | 77.2 | 0.35 | | | | | Krüger et al., 1982 |
| Agleactis cupripennis | 7.2 | ? | N | 38.2 | 0.47 | | | | | Krüger et al., 1982 |
| Agleactis cupripennis | 7.2 | ? | D | 76.2 | 1.28 | | | | | Krüger et al., 1982 |
| Boissonneana matthewsii | 7.2 | ? | N | 42.7 | 0.57 | | | | | Krüger et al., 1982 |
| Boissonneana matthewsii | 7.2 | ? | D | 74.3 | 1.10 | | | | | Krüger et al., 1982 |
| Anthracothonax nigricollis | 7.7 | ? | N | 43.4 | 0.48 | | | | | Krüger et al., 1982 |
| Anthracothonax nigricollis | 7.7 | ? | D | 82.2 | 1.29 | | | | | Krüger et al., 1982 |
| Lampornis olemenciae | 7.9 | ? | D | 35.6 | 0.87 | 1.76 | 31.0 | 37.0 | 8.8 | Lasiewski, Lasiewski, 1967 |
| Lampornis clemenciae | 8.3 | ? | N | 52.0 | 0.76 | | | | | Krüger et al., 1982 |
| Lampornis clemenciae | 8.3 | ? | D | 82.5 | 0.98 | | | | | Krüger et al., 1982 |
| Lampornis clemenciae | 8.3 | ? | N _t | 6.4 | (+0.40) | | | | | Krüger et al., 1982 |
| Eulampis jugularis | 8.4 | ? | ? | 52.8 | 1.32 | | 30.0 | | 33.4 | Hainsworth, Wolf, 1970 |
| Eulampis jugularis | 9.5 | ? | N | 54.7 | 1.07 | | | | | Krüger et al., 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|------------------------------|-------|---|----------------|-------|---------|-------|------|-------|------|---------------------------------|
| <i>Eulampis jugularis</i> | 9.5 | ? | D | 90.7 | 1.85 | | | | | Krüger et al., 1982 |
| <i>Eulampis jugularis</i> | 9.5 | ? | N _t | 8.0 | (+0.20) | | | | | Krüger et al., 1982 |
| <i>Oreotrochilus estella</i> | 8.5 | ? | N | 48.8 | 0.47 | | | | | Krüger et al., 1982 |
| <i>Oreotrochilus estella</i> | 8.5 | ? | D | 75.7 | 0.80 | | | | | Krüger et al., 1982 |
| <i>Oreotrochilus estella</i> | 8.9 | ? | N | 49.8 | 0.77 | | | | | Krüger et al., 1982 |
| <i>Oreotrochilus estella</i> | 8.9 | ? | D | 55.0 | (+0.01) | | | | | Krüger et al., 1982 |
| <i>Oreotrochilus estella</i> | 8.9 | ? | N _t | 3.0 | (+0.30) | | | | | Krüger et al., 1982 |
| <i>Patagona gigas</i> | 17.5 | ? | N | 81.1 | 1.43 | | | | | Krüger et al., 1982 |
| <i>Patagona gigas</i> | 17.5 | ? | D | 145.7 | 2.31 | | | | | Krüger et al., 1982 |
| <i>Patagona gigas</i> | 17.5 | ? | N _t | 14.7 | (+0.55) | | | | | Krüger et al., 1982 |
| <i>Patagona gigas</i> | 19.1 | ? | D | 66.6 | 1.57 | | 26.5 | | 24.7 | Lasiewski et al., 1967 |
| <i>Apus apus</i> | 44.9 | S | N | 107.6 | 2.69 | 12.56 | 26.0 | 39.0 | 37.7 | Gavrillov, 1986 |
| <u>Coliiformes</u> | | | | | | | | | | |
| <i>Colius striatus</i> | 52.5 | ? | D | 101.3 | 2.63 | 15.28 | 25.0 | 40.0 | 30.6 | Bartholomew, Trost, 1970 |
| <u>Trogoniformes</u> | | | | | | | | | | |
| <i>Trogon rufus</i> | 53 | W | N | 175.2 | 4.60 | | 30.0 | | 37.1 | Yarbrough, 1971 |
| <u>Coraciiformes</u> | | | | | | | | | | |
| <i>Merops viridis</i> | 33.8 | S | N | 66.3 | 1.23 | | 33 | | 25.7 | Bryant et al., 1984 |
| <i>Alcedo atthis</i> | 34.3 | S | N | 87.1 | 2.19 | | 25 | 38 | 32.7 | Gavrillov, Dolnik (unpublished) |
| <u>Piciformes</u> | | | | | | | | | | |
| <i>Yynx torquilla</i> | 31.8 | S | N | 77.9 | 1.95 | 6.20 | 24.0 | 37.0 | 31.0 | Gavrillov, Dolnik (unpublished) |
| <i>Dendrocopus major</i> | 98.0 | S | N | 140.3 | 3.49 | 15.50 | 18.0 | 37.0 | 77.5 | Gavrillov, 1980, 1982 |
| <i>Dendrocopus major</i> | 117.0 | W | N | 124.8 | 3.16 | 14.99 | 11.0 | 36.0 | 90.0 | Gavrillov, 1980, 1982 |
| <u>Passeriformes</u> | | | | | | | | | | |
| <i>Regulus regulus</i> | 5.5 | A | N | 34.3 | 0.875 | 3.98 | 21.0 | 38.0 | 15.9 | Gavrillov, 1972 |
| <i>Estrilda troglodytes</i> | 6.4 | ? | D | 56.5 | 1.19 | 2.83 | 38.0 | 33.80 | 11.3 | Cade et al., 1965 |
| <i>Estrilda troglodytes</i> | 6.5 | V | D | 46.5 | 1.26 | 1.55 | 28.0 | 35.0 | 10.9 | Lasiewski et al., 1964 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|-----------------------------------|------|---|---|------|------|--------|------|------|------|--------------------------------|
| <i>Lonchura striata</i> | 10.1 | S | N | 67.4 | 1.80 | 2.86 | 28.0 | 36.0 | 17.2 | Gavrilov, 1980, 1982 |
| <i>Lonchura striata</i> | 10.3 | W | N | 51.9 | 1.29 | 3.70 | 26.0 | 37.0 | 18.4 | Gavrilov, 1980, 1982 |
| <i>Vidua paradisaea</i> | 10.5 | ? | D | 48.6 | 1.21 | | 25.5 | 38.0 | 16.7 | Terroine, Trautman, 1927 |
| <i>Sylvia curruca</i> | 10.6 | S | N | 49.4 | 1.22 | 4.3 | 26.5 | 38.0 | 17.2 | Gavrilov, Dolnik (unpublished) |
| <i>Phylloscopus trochilus</i> | 10.7 | A | N | 51.9 | 1.31 | 3.60 | 26.0 | 37.0 | 18.0 | Gavrilov, Dolnik (unpublished) |
| <i>Loxops virens</i> | 10.7 | S | D | 43.2 | 0.15 | | 31.1 | | 17.9 | MacMillen, 1981 |
| <i>Arcocephalus palustris</i> | 10.8 | S | N | 57.8 | 1.44 | 3.5 | 28.0 | 37.0 | 17.6 | Gavrilov, Dolnik (unpublished) |
| <i>Parus ater</i> | 10.8 | S | N | 46.9 | 1.15 | 4.10 | 23.0 | 37.0 | 20.5 | Gavrilov, 1980, 1982 |
| <i>Parus ater</i> | 10.8 | S | D | 48.4 | 1.22 | | 21.0 | 36.0 | 22.8 | Gavrilov, 1985 |
| <i>Parus ater</i> | 11.0 | W | N | 44.4 | 1.10 | 4.69 | 19.0 | 37.0 | 23.4 | Gavrilov, 1981 |
| <i>Parus ater</i> | 11.0 | W | D | 51.9 | 1.21 | | 20.0 | 37.0 | 27.7 | Gavrilov, 1981 |
| <i>Sitta canadensis</i> | 11.2 | Y | D | 55.3 | 1.08 | 5.02 | 33.0 | 38.0 | 20.1 | Mugas, Templeton, 1970 |
| <i>Taeniopygia castanotis</i> | 11.5 | ? | D | 82.5 | 1.74 | (20.5) | 36.0 | 42.0 | 20.5 | Cade et al., 1965 |
| <i>Taeniopygia castanotis</i> | 11.7 | ? | ? | 68.2 | 1.64 | 9.2 | 29.5 | 40.0 | 18.4 | Calder, 1964 |
| <i>Taeniopygia castanotis</i> | 11.7 | S | N | 78.7 | 2.03 | 3.93 | 29.0 | 37.0 | 19.7 | Gavrilov, 1980, 1982 |
| <i>Taeniopygia castanotis</i> | 11.8 | W | N | 66.2 | 1.65 | 4.02 | 28.0 | 37.0 | 20.1 | Gavrilov, 1981 |
| <i>Taeniopygia castanotis</i> | 11.8 | W | N | 66.2 | 1.65 | 4.02 | 28.0 | 37.0 | 20.1 | Gavrilov, 1981 |
| <i>Taeniopygia castanotis</i> | 11.8 | W | D | 67.0 | 1.65 | | 27.0 | 37.0 | 22.6 | Gavrilov, 1981 |
| <i>Acrocephalus schoenobaenus</i> | 11.5 | S | N | 56.5 | 1.39 | 3.14 | 27.0 | 36.0 | 18.8 | Gavrilov, Dolnik (unpublished) |
| <i>Dendroica coronata</i> | 11.5 | W | N | 38.5 | 0.96 | | 23.2 | | 16.3 | Yarbrough, 1971 |
| <i>Ficedula hypoleuca</i> | 11.7 | A | N | 50.2 | 1.26 | 4.01 | 24.0 | 37.0 | 20.1 | Gavrilov, Dolnik (unpublished) |
| <i>Spizella passerina</i> | 11.9 | W | N | 41.0 | 1.00 | | 24.4 | | 16.7 | Yarbrough, 1971 |
| <i>Dendroica pinus</i> | 12.0 | W | N | 37.7 | 0.94 | | 23.4 | | 15.5 | Yarbrough, 1971 |
| <i>Wilsonia citrina</i> | 12.0 | S | N | 46.1 | 1.10 | | 24.9 | | 18.4 | Yarbrough, 1971 |
| <i>Empidonax virescens</i> | 12.3 | S | N | 43.1 | 1.06 | | 26.3 | | 15.5 | Yarbrough, 1971 |
| <i>Pipra mentalis</i> | 12.3 | S | N | 65.6 | 1.87 | | 27.0 | | 16.8 | Bartholomew et al., 1983 |
| <i>Hippolais icterina</i> | 12.5 | S | N | 54.0 | 1.34 | 7.26 | 24.0 | 39.0 | 21.8 | Gavrilov, Dolnik (unpublished) |
| <i>Acanthis flammea</i> | 12.8 | S | N | 40.6 | 0.82 | | 21.0 | | 22.6 | Pohl, West, 1973 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--------------------------------|--------|---|---|------|------|------|--------|------|--------|--------------------------------|
| <i>Estrilda troglodytes</i> | 7.5 | S | N | 52.3 | 1.31 | 3.24 | 30.0 | 38.0 | 13.0 | Gavrilov, 1980, 1982 |
| <i>Estrilda troglodytes</i> | 7.5 | S | D | 56.7 | 1.52 | | 28.0 | 37.0 | 14.0 | Gavrilov, 1985 |
| <i>Estrilda troglodytes</i> | 7.7 | W | N | 54.4 | 1.37 | 3.35 | 30.0 | 38.0 | 13.4 | Gavrilov, 1980, 1982 |
| <i>Estrilda troglodytes</i> | 7.7 | W | D | 64.5 | 1.56 | | 32.0 | 37.0 | 14.6 | Gavrilov, 1985 |
| <i>Auriparus flaviceps</i> | 6.8 | S | D | 30.1 | 0.64 | | 24.0 | | 14.2 | Goldstein, 1974 |
| <i>Parula americana</i> | 7.0 | S | N | 32.6 | 0.86 | | 25.7 | | 10.5 | Yarbrough, 1971 |
| <i>Tiaria canora</i> | 7.6 | S | N | 53.6 | 1.34 | 2.68 | 30.0 | 37.0 | 13.4 | Gavrilov, 1980, 1982 |
| <i>Tiaria canora</i> | 7.8 | W | N | 54.4 | 1.37 | 2.68 | 30.0 | 37.0 | 13.4 | Gavrilov, 1980, 1982 |
| <i>Loxops parva</i> | 7.9 | S | D | 40.2 | 0.83 | | 32.4 | | 12.3 | MacMillen, 1981 |
| <i>Loxops parva</i> | 8.0 | ? | D | 40.6 | 0.84 | 2.09 | 31.0 | 36.0 | 12.6 | MacMillan, 1974 |
| <i>Phylloscopus collybita</i> | 8.2 | A | N | 41.0 | 1.05 | 2.37 | 25.5 | 36.0 | 14.2 | Gavrilov, Dolnik (unpublished) |
| <i>Aegithalos caudatus</i> | 8.9 | S | N | 42.7 | 1.06 | 3.43 | 24.0 | 37.0 | 17.2 | Gavrilov, 1974, 1980, 1982 |
| <i>Aegithalos caudatus</i> | 8.8 | W | N | 41.0 | 1.01 | 4.35 | 19.0 | 37.0 | 21.8 | Gavrilov, 1974, 1980, 1980 |
| <i>Lichmera indistincta</i> | (9) | S | N | 40.2 | 0.82 | | 30.0 | | (15.6) | Collins et al., 1980 |
| <i>Lichmera indistincta</i> | (9) | S | D | 51.4 | 1.13 | | 30.0 | 40.0 | 17.8 | Collins et al., 1980 |
| <i>Troglodytes troglodytes</i> | 9.0 | S | N | 48.9 | 1.22 | 3.07 | 25.0 | 36.0 | 18.4 | Gavrilov, 1980, 1982 |
| <i>Troglodytes troglodytes</i> | 9.2 | W | N | 46.1 | 1.17 | 3.49 | 21.5 | 36.0 | 20.9 | Gavrilov, 1980, 1982 |
| <i>Uraeginthus bengalis</i> | 9.1 | S | N | 54.4 | 1.37 | 2.68 | 30.0 | 37.0 | 13.4 | Gavrilov, 1980, 1982 |
| <i>Uraeginthus bengalis</i> | 9.2 | W | N | 52.3 | 1.31 | 2.85 | 29.0 | 37.0 | 14.2 | Gavrilov, 1980, 1982 |
| <i>Phylloscopus sibilatrix</i> | 9.2 | S | N | 47.7 | 1.20 | 3.77 | 27.0 | 38.0 | 15.1 | Gavrilov, Dolnik (unpublished) |
| <i>Lonchura fuscans</i> | 9.5 | S | N | 38.4 | 1.00 | 2.77 | 30.0 | 39.0 | 8.3 | Weathers, 1977 |
| <i>Troglodytes aedon</i> | 9.7 | S | D | 61.1 | 0.95 | 5.98 | 37.8 | 37.8 | 21.5 | Kendeigh, 1939 |
| <i>Dendroica dominica</i> | 9.8 | S | N | 38.1 | 0.95 | | 25.2 | | 13.8 | Yarbrough, 1971 |
| <i>Dendroica palmarum</i> | 9.8 | W | N | 31.4 | 0.77 | | 23.3 | | 13.4 | Yarbrough, 1971 |
| <i>Parus atricapillus</i> | (10.3) | S | W | 55.7 | 1.32 | | 26.0 | | 21.8 | Rising, Hudson, 1974 |
| <i>Parus atricapillus</i> | 10.3 | W | N | 43.4 | 0.85 | | (26.0) | | 21.8 | Rising, Hudson, 1974 |
| <i>Parus atricapillus</i> | 11.2 | S | N | 40.2 | 1.13 | | 17.4 | | 20.5 | Chaplin, 1974 |
| <i>Parus atricapillus</i> | 11.6 | W | N | 38.9 | 1.16 | | 14.8 | | 21.8 | Chaplin, 1974 |
| <i>Parus atricapillus</i> | 12.0 | W | N | 46.9 | 0.82 | | 14.4 | | 35.2 | Grossman, West, 1977 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---------------------------|------|------|---|------|------|------|------|------|------|--------------------------------|
| Acanthis flammea | 13.2 | S | D | 50.2 | 1.04 | | 23.0 | | 24.7 | West, 1972 |
| Acanthis flammea | 13.8 | W | D | 50.7 | 1.46 | | 7.0 | | 40.6 | Pohl, West, 1973 |
| Acanthis flammea | 14.0 | S | N | 51.9 | 1.29 | 3.09 | 21.0 | 34.0 | 24.7 | Gavrilov, 1974, 1980, 1982 |
| Acanthis flammea | 14.3 | W | N | 59.9 | 1.31 | 3.66 | 17.0 | 34.0 | 29.3 | Gavrilov, 1974, 1980, 1982 |
| Acanthis flammea | 15.6 | W | N | 44.4 | 0.86 | | 11.5 | | 34.7 | Pohl, West, 1973 |
| Protonotaria citrea | 12.8 | S | N | 51.1 | 1.26 | | 26.9 | | 17.2 | Yarbrough, 1971 |
| Spinus tristis | 14.5 | W | N | 49.3 | 1.12 | 4.64 | 15.0 | 35.0 | 32.5 | Dawson, Carey, 1976 |
| Himatione sanguinea | 12.9 | S | D | 39.9 | 0.76 | | 25.1 | | 21.5 | MacMillen, 1981 |
| Phoenicurus phoenicurus | 13.0 | S, A | N | 50.2 | 1.26 | 5.02 | 24.0 | 38.0 | 20.1 | Gavrilov, Dolnik (unpublished) |
| Serinus canaria | 13.3 | A | N | 49.4 | 1.25 | 3.28 | 24.0 | 36.0 | 19.7 | Gavrilov, Dolnik (unpublished) |
| Riparia riparia | 13.6 | A | N | 56.9 | 1.41 | 4.02 | 26.0 | 37.0 | 20.1 | Gavrilov, 1986 |
| Ammodramus savannarum | 13.8 | W | N | 44.8 | 1.16 | | 25.3 | | 15.5 | Yarbrough, 1971 |
| Phoenicurus ochruros | 13.9 | S | N | 52.3 | 1.31 | 5.23 | 24.0 | 38.0 | 20.9 | Gavrilov, Dolnik (unpublished) |
| Spinus spinus | 14.0 | S | N | 52.8 | 1.31 | 5.02 | 21.0 | 37.0 | 25.1 | Gavrilov, 1980, 1982 |
| Spinus spinus | 14.0 | S | D | 56.0 | 1.49 | | 19.0 | 36.0 | 27.6 | Gavrilov, 1985 |
| Spinus spinus | 14.2 | W | N | 51.9 | 1.30 | 4.74 | 18.0 | 36.0 | 28.5 | Gavrilov, 1981 |
| Spinus spinus | 14.2 | W | D | 57.4 | 1.36 | | 19.0 | 35.0 | 31.4 | Gavrilov, 1981 |
| Hirundo tahitica | 14.1 | S | N | 59.8 | 1.48 | | 30.0 | | 15.3 | Bryant et al., 1984 |
| Saxicola rubetra | 14.3 | S | N | 59.0 | 1.46 | 5.23 | 26.0 | 38.0 | 20.9 | Gavrilov, Dolnik (unpublished) |
| Muscicapa striata | 14.4 | S | N | 60.3 | 1.51 | 5.34 | 26.0 | 38.0 | 21.3 | Gavrilov, Dolnik (unpublished) |
| Motacilla flava | 14.7 | S | N | 63.2 | 1.59 | 5.55 | 26.0 | 38.0 | 22.2 | Gavrilov, Dolnik (unpublished) |
| Tarsiger cyanurus | 14.8 | W | N | 45.2 | 1.21 | 4.10 | 22.0 | 37.0 | 20.5 | Gavrilov (unpublished) |
| Melospiza georgiana | 14.9 | W | N | 46.9 | 1.18 | | 24.1 | | 18.4 | Yarbrough, 1971 |
| Vestiaria coccinea | 15.0 | S | D | 51.2 | 1.00 | | 24.9 | | 26.8 | MacMillen, 1981 |
| Viridonia virens | 15.3 | ? | D | 49.4 | 0.80 | | 30.0 | | 25.5 | MacMillen, 1974 |
| Manacus vittelinus | 15.5 | S | N | 62.5 | 1.72 | | 25.0 | | 20.1 | Bartholomew et al., 1983 |
| Passercula sandwichensis | 15.9 | W | N | 45.2 | 1.13 | | 22.6 | | 19.3 | Yarbrough, 1971 |
| Passercula. sandwichensis | 17.4 | W | N | 78.3 | 1.74 | | 30.0 | | 25.6 | Williams, Hamsell, 1981 |
| Parus major | 16.4 | S | N | 62.4 | 1.56 | 4.76 | 22.0 | 36.0 | 28.5 | Gavrilov, 1980, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|-------------------------------|------|---|---|------|------|------|------|------|------|--|
| <i>Parus major</i> | 16.4 | S | D | 67.5 | 1.80 | | 20.0 | 34.0 | 31.6 | Gavrillov, 1985 |
| <i>Parus major</i> | 17.1 | W | N | 58.6 | 1.46 | 5.37 | 18.0 | 36.0 | 32.2 | Gavrillov, 1981 |
| <i>Parus major</i> | 17.1 | W | D | 62.8 | 1.51 | | 18.0 | 35.0 | 35.6 | Gavrillov, 1981 |
| <i>Parus major</i> | 18.0 | W | N | 43.1 | 0.85 | 3.12 | 15.0 | 33.0 | 28.0 | J.A.L.Mertens (personal communication) |
| <i>Parus major</i> | 18.4 | W | ? | 50.7 | 0.53 | 2.97 | 28.0 | 31.0 | 32.7 | Hissa, Palokangas, 1970 |
| <i>Parus major</i> | 19.0 | S | ? | 85.4 | 2.21 | 3.53 | 29.0 | 33.0 | 31.8 | Hissa, Palokangas, 1970 |
| <i>Carduelis carduelis</i> | 16.5 | W | N | 53.2 | 1.39 | 6.03 | 16.5 | 37.0 | 30.1 | Gavrillov, 1982b |
| <i>Prunella modularis</i> | 16.8 | A | N | 62.4 | 1.56 | 4.68 | 22.0 | 36.0 | 28.1 | Gavrillov, Dolnik(unpublished) |
| <i>Acanthis cannabina</i> | 16.9 | A | N | 62.8 | 1.60 | 4.89 | 21.0 | 36.0 | 29.3 | Gavrillov, 1982b |
| <i>Emberiza schoeniclus</i> | 17.6 | A | N | 60.3 | 1.49 | 4.32 | 23.0 | 36.0 | 26.0 | Gavrillov, 1982b |
| <i>Erithacus rubecula</i> | 17.6 | S | N | 73.7 | 1.76 | 5.19 | 25.0 | 37.0 | 26.0 | Gavrillov, 1980, 1982 |
| <i>Erithacus rubecula</i> | 17.6 | S | D | 78.1 | 2.13 | | 23.0 | 36.0 | 29.1 | Gavrillov, 1985 |
| <i>Erithacus rubecula</i> | 17.6 | W | N | 65.3 | 1.64 | 4.86 | 25.0 | 37.0 | 24.3 | Gavrillov, 1981 |
| <i>Erithacus rubecula</i> | 17.6 | W | D | 74.0 | 1.90 | | 25.0 | 36.0 | 26.4 | Gavrillov, 1981 |
| <i>Parus varius</i> | 17.7 | W | N | 59.0 | 1.48 | 5.15 | 19.0 | 36.0 | 31.0 | Gavrillov (unpublished) |
| <i>Parus varius</i> | 17.7 | W | D | 62.4 | 1.40 | | 18.0 | 36.0 | 37.2 | Gavrillov (unpublished) |
| <i>Hirundo rustica</i> | 18.0 | S | N | 94.6 | 2.36 | | 29.5 | | 27.2 | Keskpai, 1968 |
| <i>Hirundo rustica</i> | 18.4 | S | N | 74.3 | 2.20 | 6.50 | 22.0 | 38.0 | 26.0 | Gavrillov, 1986 |
| <i>Motacilla alba</i> | 18.0 | S | N | 64.5 | 1.60 | 4.31 | 24.0 | 36.0 | 26.0 | Gavrillov, 1980, 1982 |
| <i>Motacilla alba</i> | 18.2 | W | N | 62.4 | 1.59 | 4.05 | 24.0 | 36.0 | 24.3 | Gavrillov, 1980, 1982 |
| <i>Melospiza melodia</i> | 19.1 | W | N | 54.4 | 1.33 | | 24.5 | | 21.8 | Yarbrough, 1971 |
| <i>Seiurus noveboracensis</i> | 18.7 | A | N | 61.5 | 1.46 | | 25.5 | | 21.8 | Yarbrough, 1971 |
| <i>Authus pratensis</i> | 18.9 | S | N | 66.1 | 1.67 | 6.50 | 24.0 | 38.0 | 26.0 | Gavrillov, 1982b |
| <i>Seiurus aurocapillus</i> | 19.0 | A | N | 46.5 | 1.12 | | 22.9 | | 20.9 | Yarbrough, 1971 |
| <i>Anthus trivialis</i> | 19.7 | A | N | 73.7 | 1.85 | 4.88 | 24.0 | 36.0 | 29.3 | Gavrillov, 1982b |
| <i>Zonotrichia albicollis</i> | 20.2 | W | N | 57.4 | 1.40 | | 23.6 | | 24.3 | Yarbrough, 1971 |
| <i>Zonotrichia albicollis</i> | 22.5 | ? | N | 62.0 | 1.82 | 2.45 | 20.0 | 35.0 | 17.2 | Hudson, Kimzey, 1964 |
| <i>Delichon urbica</i> | 20.5 | S | N | 92.5 | 2.31 | | 29.5 | | 30.6 | Keskpai, 1968 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--------------------------|--------|---|---|------|------|------|------|------|------|----------------------|
| Luscinia svecica | 20.8 | S | N | 73.3 | 1.84 | 7.75 | 23.0 | 38.0 | 31.0 | Gavrilov, 1982b |
| Fringilla coelebs | 21.0 | S | N | 73.3 | 1.82 | 5.37 | 22.5 | 36.0 | 32.2 | Gavrilov, 1980, 1982 |
| Fringilla coelebs | 21.0 | S | D | 78.5 | 1.98 | | 20.0 | 36.0 | 39.0 | Gavrilov, 1985 |
| Fringilla coelebs | 20.8 | W | N | 77.0 | 1.95 | 6.35 | 20.0 | 36.0 | 38.1 | Gavrilov, 1981 |
| Fringilla coelebs | 20.8 | W | D | 87.9 | 2.11 | | 22.0 | 35.0 | 41.5 | Gavrilov, 1981 |
| Fringilla montifringilla | 21.0 | A | N | 67.0 | 1.65 | 5.51 | 20.0 | 36.0 | 33.1 | Gavrilov, 1982b |
| Sylvia nisoria | 21.3 | S | N | 77.9 | 1.95 | 8.27 | 23.0 | 38.0 | 33.1 | Gavrilov, 1982b |
| Sylvia nisoria | 21.4 | A | N | 70.2 | 1.92 | 5.60 | 22.0 | 37.0 | 28.0 | Gavrilov, 1982b |
| Carpodacus erythrinus | 21.2 | S | N | 85.0 | 2.13 | 7.95 | 25.0 | 38.0 | 31.8 | Gavrilov, 1980, 1982 |
| Carpodacus erythrinus | 21.2 | S | D | 94.2 | 2.50 | | 23.0 | 37.0 | 36.6 | Gavrilov, 1985 |
| Carpodacus erythrinus | 21.6 | W | N | 78.3 | 1.97 | 7.74 | 24.0 | 38.0 | 31.0 | Gavrilov, 1981 |
| Carpodacus erythrinus | 21.6 | W | D | 81.2 | 2.00 | | 24.0 | 36.0 | 33.1 | Gavrilov, 1981 |
| Poecetes gramineus | 21.5 | W | N | 55.3 | 1.40 | | 22.5 | | 23.4 | Yarbrough, 1971 |
| Sayornis phoebe | 21.6 | W | N | 69.1 | 1.70 | | 23.3 | | 29.7 | Yarbrough, 1971 |
| Anthus campestris | 21.8 | S | N | 73.3 | 1.83 | 8.27 | 22.0 | 38.0 | 38.1 | Gavrilov, 1981b |
| Sylvia atricapilla | 21.9 | A | N | 71.2 | 1.76 | 7.20 | 20.0 | 37.0 | 36.0 | Gavrilov, 1981b |
| Emberiza hortulana | 22.0 | W | ? | 78.3 | 1.57 | 9.11 | 25.0 | 38.0 | 36.4 | Wallgren, 1954 |
| Emberiza hortulana | 24.3 | S | N | 86.7 | 2.20 | 9.00 | 23.0 | 38.0 | 36.0 | Gavrilov, 1980, 1982 |
| Emberiza hortulana | 27.0 | W | N | 78.7 | 1.98 | 7.03 | 22.0 | 37.0 | 35.2 | Gavrilov, 1980, 1982 |
| Passer montanus | 22.0 | S | N | 75.4 | 1.80 | 6.80 | 23.0 | 37.0 | 34.0 | Gavrilov, 1981b |
| Passer montanus | 22.3 | A | N | 69.9 | 1.74 | 5.86 | 20.0 | 36.0 | 35.2 | Gavrilov, 1981b |
| Passer d.bactrianus | 23.0 | S | N | 75.4 | 1.89 | 7.95 | 23.0 | 38.0 | 31.8 | Gavrilov, 1980, 1982 |
| Passer d.bactrianus | 23.2 | W | N | 75.4 | 1.89 | 7.95 | 23.0 | 38.0 | 31.8 | Gavrilov, 1980, 1982 |
| Sylvia borin | 24.8 | A | N | 79.5 | 1.98 | 6.00 | 22.0 | 36.0 | 36.0 | Gavrilov, 1982b |
| Catharus minimus | 24.8 | S | D | 64.3 | 0.97 | | 25.5 | | 39.6 | Holmes, Sawyer, 1975 |
| Meliphaga virescens | (25.0) | S | N | 43.7 | 0.60 | | 30.0 | | 25.6 | Collins et al., 1980 |
| Meliphaga virescens | (25.0) | S | N | 77.4 | 1.57 | | 30.0 | 40 | 30.5 | Collins et al., 1980 |
| Passer domesticus | 25.1 | W | D | 94.2 | 1.49 | 7.79 | 37.0 | 37.0 | 38.9 | Kendeigh, 1944 |
| Passer domesticus | 25.3 | ? | N | 86.7 | 1.54 | 7.03 | 22.0 | 37.0 | 35.2 | Hudson, Kimzey, 1966 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--|------|---|---|------|------|------|------|------|------|-----------------------|
| <i>Passer domesticus</i> | 25.5 | ? | N | 64.9 | 1.77 | 5.78 | 21.0 | 37.0 | 28.9 | Hudson, Kimzey, 1966 |
| <i>Passer domesticus</i> | 26.5 | S | N | 92.1 | 2.27 | 8.21 | 22.5 | 37.0 | 41.0 | Gavrillov, 1980, 1982 |
| <i>Passer domesticus</i> | 26.5 | S | D | 96.5 | 2.46 | | 20.0 | 36.0 | 47.2 | Gavrillov, 1985 |
| <i>Passer domesticus</i> | 26.4 | W | N | 90.4 | 2.29 | 7.05 | 21.0 | 36.0 | 42.3 | Gavrillov, 1981 |
| <i>Passer domesticus</i> | 26.4 | W | D | 94.6 | 2.30 | | 22.0 | 35.0 | 44.8 | Gavrillov, 1981 |
| <i>Eremophilla alpestris</i> | 26.0 | S | N | 56.1 | 1.26 | 4.06 | 22.0 | 35.0 | 28.5 | Trost, 1972 |
| <i>Eremophilla alpestris</i> | 26.0 | S | D | 66.6 | 1.13 | | 35.0 | | 26.8 | Trost, 1972 |
| <i>Lonotrichia leucophrys gambelii</i> | 26.0 | W | N | 60.3 | 1.28 | | 22.2 | | 33.1 | Maxwell, King, 1980 |
| <i>Lonotrichia leucophrys gambelii</i> | 26.1 | W | N | 60.3 | 1.50 | | 20.6 | | 29.3 | Yarbrough, 1971 |
| <i>Lonotrichia leucophrys gambelii</i> | 28.6 | S | N | 72.8 | 1.72 | 6.70 | 23.0 | 37.0 | 33.5 | King, 1964 |
| <i>Lonotrichia leucophrys gambelii</i> | 27.3 | W | N | 62.0 | 1.49 | | 23.3 | | 29.3 | Maxwell, King, 1976 |
| <i>Emberiza citrinella</i> | 26.4 | W | ? | 68.7 | 1.23 | 4.23 | 25.0 | 33.0 | 38.1 | Wallgren, 1954 |
| <i>Emberiza citrinella</i> | 26.8 | S | N | 77.5 | 1.94 | 7.54 | 20.5 | 37.0 | 37.7 | Gavrillov, 1980, 1982 |
| <i>Emberiza citrinella</i> | 26.8 | S | N | 82.6 | 2.07 | | 19.0 | 36.0 | 43.3 | Gavrillov, 1985 |
| <i>Emberiza citrinella</i> | 27.4 | W | N | 71.6 | 1.78 | 7.18 | 16.0 | 36.0 | 43.1 | Gavrillov, 1981 |
| <i>Emberiza citrinella</i> | 27.4 | W | D | 87.5 | 2.24 | | 17.0 | 35.0 | 49.4 | Gavrillov, 1981 |
| <i>Lanius collurio</i> | 27.0 | S | N | 82.9 | 2.08 | 6.61 | 24.0 | 37.0 | 33.1 | Gavrillov, 1982b |
| <i>Catharus guttata</i> | 27.8 | S | D | 82.5 | 1.65 | | 25.0 | | 41.0 | Holmes, Sawyer, 1975 |
| <i>Catharus ustulatus</i> | 27.9 | S | D | 85.0 | 1.87 | | 24.0 | | 40.2 | Holmes, Sawyer, 1975 |
| <i>Chloris chloris</i> | 28.2 | S | N | 81.2 | 2.03 | 6.84 | 20.0 | 36.0 | 41.0 | Gavrillov, 1980, 1982 |
| <i>Chloris chloris</i> | 28.2 | S | D | 88.6 | 2.62 | | 16.0 | 35.0 | 46.4 | Gavrillov, 1985 |
| <i>Chloris chloris</i> | 29.0 | W | N | 80.4 | 2.15 | 8.03 | 16.0 | 36.0 | 48.1 | Gavrillov, 1981 |
| <i>Chloris chloris</i> | 29.0 | W | D | 86.9 | 2.21 | | 17.0 | 35.0 | 51.9 | Gavrillov, 1981 |
| <i>Catharus fuscescens</i> | 28.0 | S | D | 91.9 | 1.55 | | 31.0 | | 43.5 | Holmes, Sawyer, 1975 |
| <i>Loxia curvirostra</i> | 29.4 | W | N | 69.5 | 1.70 | | 17.0 | 36.0 | 44.0 | Dawson, Tordoff, 1964 |
| <i>Loxia curvirostra</i> | 39.4 | S | N | 90.0 | 2.24 | 8.65 | 13.0 | 36.0 | 51.9 | Gavrillov, 1980, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--------------------------------------|--------|-----|---|-------|------|---------|------|------|-------|---------------------------|
| <i>Loxia curvirostra</i> | 42.7 | W | N | 86.2 | 2.16 | 8.31 | 14.0 | 35.0 | 58.2 | Gavrilov, 1980, 1982 |
| <i>Loxia leucoptera</i> | 29.8 | W | N | 62.4 | 1.58 | | 14.0 | | 40.2 | Dawson, Tordoff, 1964 |
| <i>Pyrrhula pyrrhula</i> | 30.4 | W | N | 80.0 | 2.15 | 7.95 | 15.0 | 36.0 | 47.7 | Gavrilov, 1982b |
| <i>Cardinalis sinuata</i> | 32.0 | S | N | 99.6 | 2.21 | | 29.7 | 42.8 | 33.9 | Hinds, Calder, 1973 |
| <i>Psittirostra centanus</i> | (32.8) | W | N | 80.6 | 1.53 | 69.3 | 23.5 | 36.5 | 38.1 | Weathers, van Riper, 1982 |
| <i>Lonotrichia querula</i> | 33.0 | A,W | ? | 146.9 | 2.58 | | 33.0 | | 55.7 | Rising, 1968 |
| <i>Lonotrichia querula</i> | 33.3 | W | N | 78.3 | 1.91 | 11.13 | 20.7 | 37.0 | 42.7 | Yarbrough, 1971 |
| <i>Lullula arborea</i> | 33.2 | A | N | 86.2 | 2.14 | 7.05 | 20.5 | 36.0 | 42.3 | Gavrilov, 1982b |
| <i>Psittirostra bailleni</i> | (36.0) | W | N | 74.3 | 1.90 | 3.51 | 17.5 | 31.0 | 38.7 | Weathers, van Riper, 1982 |
| <i>Molothrus ater</i> | 42.5 | ? | ? | 140.3 | 2.95 | (43.54) | 28.7 | 42.6 | 43.5 | Hinds, Calder, 1973 |
| <i>Myarchus crinitus</i> | 33.9 | S | N | 80.8 | 1.96 | | 24.3 | | 33.1 | Yarbrough, 1971 |
| <i>Cardinalis cardinalis</i> | 41.0 | W | ? | 86.7 | 1.94 | 5.69 | 18.0 | 33.0 | 51.1 | Dawson, 1958 |
| <i>Cardinalis cardinalis</i> | 41.0 | S | N | 127.7 | 2.95 | (43.54) | 28.7 | 42.6 | 43.5 | Hinds, Calder, 1973 |
| <i>Pipilo fuscus</i> | 43.7 | ? | ? | 125.6 | 3.14 | 8.21 | 23.0 | 34.0 | 57.4 | Dawson, 1954 |
| <i>Pipilo aberti</i> | 46.6 | ? | ? | 155.8 | 3.89 | 8.96 | 25.0 | 35.0 | 62.8 | Dawson, 1954 |
| <i>Agelaius phoeniceus</i> ♀ | 46.5 | W | D | 179.6 | 2.47 | | | | | Lewis, Dyer, 1969 |
| <i>Agelaius phoeniceus</i> ♀ | 46.5 | W | N | 73.3 | 0.42 | | | | | Lewis, Dyer, 1969 |
| <i>Agelaius phoeniceus</i> ♂ | 70.3 | W | D | 191.3 | 3.22 | 51.08 | 27.5 | 40.0 | 102.2 | Lewis, Dyer, 1969 |
| <i>Agelaius phoeniceus</i> ♂ | 70.3 | W | N | 123.1 | 1.31 | | | | | Lewis, Dyer, 1969 |
| <i>Coccothraustes coccothraustes</i> | 48.3 | A | N | 105.1 | 2.63 | 8.61 | 17.0 | 36.0 | 60.3 | Gavrilov, 1982b |
| <i>Hylocichla mystelina</i> | 48.3 | S | D | 110.1 | 2.44 | | 21.0 | | 58.6 | Holmes, Sawyer, 1975 |
| <i>Cinclus mexicanus</i> | 50.2 | ? | ? | 58.2 | 1.57 | 4.98 | 11.5 | 34.0 | 39.8 | Murriah, 1970 |
| <i>Loxia pytiopsittacus</i> | 53.7 | W | N | 100.5 | 2.51 | 9.87 | 12.5 | 35.0 | 69.1 | Gavrilov, 1982b |
| <i>Coccothraustes vespertina</i> | 54.5 | Y | N | 118.5 | 2.24 | 8.92 | 25.0 | 35.0 | 62.4 | West, Hart, 1966 |
| <i>Coccothraustes vespertina</i> | 54.5 | Y | D | 192.6 | 2.52 | | | | | West, Hart, 1966 |
| <i>Coccothraustes vespertina</i> | 55.3 | W | N | 107.2 | 2.61 | 9.34 | 16.0 | 35.0 | 65.3 | Dawson, Tordoff, 1959 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--------------------------------|-------|---|---|-------|------|-------|------|------|-------|----------------------------------|
| <i>Turdus iliacus</i> | 58.0 | W | N | 125.6 | 3.16 | 10.4 | 20.0 | 36.0 | 62.4 | Gavrilov, 1979, 1981 |
| <i>Turdus iliacus</i> | 58.0 | W | D | 140.7 | 3.40 | | 20.0 | 35.0 | 72.8 | Gavrilov, 1981 |
| <i>Turdus philomelos</i> | 62.8 | S | N | 132.3 | 3.31 | 12.56 | 21.0 | 37.0 | 62.8 | Gavrilov, 1979, 1980, 1982 |
| <i>Turdus philomelos</i> | 62.8 | S | D | 136.5 | 3.45 | | 19.0 | 36.0 | 71.0 | Gavrilov, 1985 |
| <i>Turdus philomelos</i> | 64.0 | W | N | 125.6 | 3.09 | 10.89 | 19.5 | 36.0 | 65.3 | Gavrilov, 1979, 1980, 1981, 1982 |
| <i>Turdus philomelos</i> | 64.0 | W | D | 137.3 | 3.12 | | 20.0 | 35.0 | 74.9 | Gavrilov, 1982 |
| <i>Oriolus orolus</i> | 64.9 | S | N | 123.9 | 3.10 | 11.22 | 22.0 | 37.0 | 56.1 | Gavrilov, 1982b |
| <i>Perisoreus canadensis</i> | 71.2 | S | N | 108.0 | 0.98 | | 36.0 | | 58.6 | Veghte, 1964 |
| <i>Perisoreus canadensis</i> | 71.2 | A | N | 98.4 | 1.95 | | 9.0 | | 58.6 | Veghte, 1964 |
| <i>Perisoreus canadensis</i> | 71.2 | W | N | 83.7 | 1.92 | | 7.0 | | 58.6 | Veghte, 1964 |
| <i>Perisoreus canadensis</i> | 71.2 | V | N | 88.8 | 2.32 | | 7.0 | | 58.6 | Veghte, 1964 |
| <i>Lanius excubitor</i> | 72.4 | A | N | 127.7 | 3.18 | 10.04 | 18.0 | 35.0 | 70.3 | Gavrilov, 1982b |
| <i>Bombycilla garrulus</i> | 72.5 | A | N | 124.8 | 3.02 | 11.79 | 14.0 | 35.0 | 82.5 | Gavrilov, Dolnik(unpublished) |
| <i>Sturnus vulgaris</i> | 75.0 | A | N | 136.5 | 3.47 | 12.91 | 17.0 | 36.0 | 77.5 | Gavrilov, 1982b |
| <i>Sturnus vulgaris</i> | 88.2 | Y | N | 175.0 | 4.30 | | 14.7 | | 111.8 | Gohnson, McTaggart, 1975 |
| <i>Pinicola enucleator</i> | 78.4 | W | N | 137.3 | 2.09 | 13.40 | 13.0 | 35.0 | 93.8 | Gavrilov, Dolnik(unpublished) |
| <i>Cyanocitta cristata</i> | 80.8 | ? | N | 103.0 | 1.72 | | 18.0 | | 72.0 | Misch, 1960 |
| <i>Turdus merula</i> | 82.6 | S | N | 139.0 | 3.45 | 13.40 | 17.0 | 36.0 | 80.4 | Gavrilov, 1979, 1980, 1982 |
| <i>Turdus merula</i> | 82.6 | S | D | 148.4 | 3.67 | | 15.0 | 34.0 | 93.3 | Gavrilov, 1985 |
| <i>Turdus merula</i> | 83.0 | W | N | 137.8 | 3.44 | 12.80 | 14.0 | 35.0 | 89.6 | Gavrilov, 1979, 1980, 1982 |
| <i>Turdus merula</i> | 83.0 | W | D | 147.4 | 3.49 | | 12.0 | 35.0 | 105.5 | Gavrilov, 1981 |
| <i>Turdus viscivorus</i> | 108.2 | W | N | 155.8 | 3.77 | 19.09 | 16.0 | 37.0 | 95.5 | Gavrilov, 1979 |
| <i>Sturnus cristatellus</i> | 109.4 | Y | N | 169.1 | 4.24 | | 15.3 | | 104.3 | Gohnson, McTaggart, 1975 |
| <i>Nucifraga caryocatactes</i> | 147.0 | W | N | 189.2 | 4.86 | 19.40 | 15.0 | 36.0 | 116.4 | Gavrilov, 1979 |
| <i>Garrulus glandarius</i> | 153.0 | W | N | 190.1 | 4.69 | 19.97 | 15.0 | 36.0 | 119.7 | Gavrilov, 1979 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|--------------------------|--------|---|-----|-------|-------|-------|------|------|--------|----------------------------------|
| Pica pica | 202.0 | W | N | 221.1 | 6.22 | 24.79 | 13.0 | 36.0 | 148.6 | Gavrilov, 1979 |
| Coleus monedula | 209.0 | S | N | 238.0 | 5.93 | 26.24 | 18.0 | 37.0 | 131.2 | Gavrilov, 1985 |
| Coleus monedula | 209.0 | S | D | 244.6 | 6.00 | | 16.0 | 36.0 | 151.2 | Gavrilov, 1985 |
| Coleus monedula | 215.0 | W | N | 222.7 | 5.63 | 26.80 | 11.0 | 36.0 | 160.8 | Gavrilov, 1979, 1981 |
| Coleus monedula | 215.0 | W | D | 241.2 | 6.53 | | 11.0 | 35.0 | 167.5 | Gavrilov, 1981 |
| Corvus brachyrhynchos | 384.8 | W | (N) | 408.2 | 8.29 | 63.10 | 15.0 | 37.5 | 284.0 | Wunder, Trebella, 1976 |
| Corvus frugilegus | 390.0 | W | N | 302.7 | 7.66 | 37.68 | 10.0 | 36.0 | 226.1 | Gavrilov, 1979 |
| Corvus corone cornix | 518.0 | S | N | 394.4 | 9.78 | 47.82 | 11.0 | 36.0 | 286.8 | Gavrilov, 1979, 1980, 1982 |
| Corvus corone cornix | 518.0 | S | D | 422.6 | 10.31 | | 9.0 | 35.0 | 329.8 | Gavrilov, 1985 |
| Corvus corone cornix | 540.0 | W | N | 388.1 | 9.55 | 55.13 | 6.0 | 36.0 | 330.8 | Gavrilov, 1979, 1980, 1981, 1982 |
| Corvus corone cornix | 540.0 | W | D | 422.9 | 9.00 | | 4.0 | 35.0 | 386.9 | Gavrilov, 1981 |
| Corvus ruficollis | 660.0 | W | N | 391.5 | 9.80 | 58.70 | 10.0 | 37.0 | 293.5 | Gavrilov, 1979 |
| Corvus corax principalis | 1097 | S | D | | 16.87 | | | | 844.1 | Schwan, Williams, 1978 |
| Corvus corax principalis | 1174 | W | D | | 16.16 | | | | 1138.3 | Schwan, Williams, 1978 |
| Corvus corax | 1185.0 | W | N | 578.6 | 12.70 | 83.74 | 6.0 | 36.0 | 502.4 | Dolnik, 1974 |
| Corvus corax | 1203.0 | S | N | 629.7 | 15.37 | 79.34 | 10.0 | 36.0 | 476.1 | Gavrilov, 1979, 1980, 1981, 1982 |
| Corvus corax | 1203.0 | S | D | 686.3 | 16.73 | | 10.0 | 35.0 | 518.9 | Gavrilov, 1985 |
| Corvus corax | 1208 | W | N | 574.5 | 14.03 | 86.39 | 4.0 | 36.0 | 518.3 | Gavrilov, 1979, 1980, 1982 |
| Corvus corax | 1208 | W | D | 642.3 | 15.41 | | 2.0 | 35.0 | 618.0 | Gavrilov, 1981 |

The next symbols are used in the tables:

- m - avian body mass (g) in experimental birds or common body mass of the same species if the body mass in experimental birds was unknown
- D - measurements were made during the active (day-time) phase of the avian circadian cycle
- N - measurements were made during the resting (night-time) phase of the avian circadian cycle
- W - measurements were made during the nonproductive "winter" phase of the avian annual cycle
- S - measurements were made during the reproductive "summer" phase of the avian annual cycle
- A - measurements were made during the nonproductive "autumnal" (after moult) phase of the avian annual cycle
- V - measurements were made during the early part of the productive "vernal" phase of the avian annual cycle
- Y - measurements were made during the whole year

The data on the standard metabolic rate and thermal conductance were presented in forms of:

$$BM = SM_0 - h_1 T_a; \quad h_1 = \frac{SM_0 - BM}{T_{lc}}$$

$$SM_0 = h_1 m (T_b - T_a), \text{ where } T_b \text{ at } T_a = T_{lc};$$

$$T_x = \frac{SM_0}{h_1};$$

$$h_u = \frac{BM}{T_b - T_{uc}}, \text{ where } T_b \text{ at } T_a = T_{uc} = 42^\circ\text{C}.$$

II. BASAL METABOLIC RATE IN BIRDS ONLY: WORLD DATA

Some publications contain only data on the basal metabolic rate in birds. These data on BM are interesting because of (a) species are new, (b) measurements are original, (c) phases of circadian or annual cycles are new, (d) species are rare or interesting in relation to their systematic position, ecological properties or their body mass, (e) experimental birds originate from another part of the species area.

Additional data on basal metabolic rate that listed in the table increase the number of studied species up to 790. It is 5.5 times more than that in the check-list of Lasiewski and Dawson (1967) and 2.5 times more than that in the check-list of Kendeigh et al. (1977).

However some data presented in the Table 2 were obtained in unknown or quasi-standard conditions, physiological state of experimental birds could be abnormal, and phases of circadian cycle and annual cycle were unknown. Therefore it limits the using of these data for the converting daily energy budget of species from DM units to energy units. BM rate as it is predicted by allometric equations on the base of the body mass may be more adequate to the actual basal metabolic rate of species than some measured values of BM in this species.

T a b l e 2. Additional data on the basal metabolic rate

| Species | Body mass, g | Season | Time of measurements | BM, kJ bird ⁻¹ day ⁻¹ | References |
|----------------------------|--------------------|--------|-------------------------|--|---|
| 1 | 2 | 3 | 4 | 5 | 6 |
| <u>Sphenisciformes</u> | | | | | |
| Eudyptes albosignata | 1150 | ? | ? | 571.4 | Pinshow et al., 1977 |
| Eudyptes pachyrhynchus | 2600 | ? | ? | 598.7 | Drent, Stonehouse, 1971 |
| Pygoscelis adeliae | 3890 | S | D | 1041.1 | Fadak et al., 1974 |
| Pygoscelis adeliae | 3500 | ? | ? | 1217.3 | Resche, Boyd, 1969 |
| Pygoscelis adeliae | 3500 | S | N | 1582.3 | Ricklefs, Matthew, 1983 |
| Pygoscelis adeliae | 3900 | ? | ? | 1053.6 | Kooyman et al., 1976 |
| Eudyptes chrysolophus | 4200 | ? | D | 1958.1 | Scholander et al., 1940 |
| Spheniscus humboldti | 4500 | S | D | 1726.7 | Butler, Voakes, 1984 |
| Pygoscelis papua | 5700 | ? | D | 2832.2 | Scholander et al., 1940 |
| Pygoscelis papua | 5850 | ? | D | 2906.7 | Scholander et al., 1940 |
| Aptenodytes patagonica | (1100) | S | D | 2244.7 | Groscolas et al., 1982 |
| Aptenodytes patagonica | 13000 | ? | ? | 2953.0 | Le Maho, Despin, 1976 |
| Aptenodytes patagonica | 12600 | S | D | 869.4 | Barré, 1980 |
| Aptenodytes forsteri | (23000) | S | D | 4388.0 | Groscolas et al., 1982 |
| <u>Struthioniformes</u> | | | | | |
| Struthio camelus | 100000 | ? | ? | 9839.5 | Grawford, Schmidt-Nielsen, 1967 |
| <u>Rheiformes</u> | | | | | |
| Rhea americana | 21700 | ? | ? | 3311.9 | Grawford, Lasiewski, 1968 |
| <u>Casuariformes</u> | | | | | |
| Casuarus bennetti | 17600 | ? | N | 2160.5 | Benedict, Fox, 1927 |
| Dromiceus novae-hollandiae | 38030 | S | ? | 4337.7 | Grawford, Lasiewski, 1968 |
| Dromiceus novae-hollandiae | 38925 | S | ? | 3752.6 | Calder, Dawson, 1978 |
| <u>Procellariiformes</u> | | | | | |
| Oceanodroma leucorhoa | 42.0 | ? | ? | 53.06 | Iversen, Krog, 1972 |
| Oceanodroma leucorhoa | 43.5 | S | N | 60.9 | Ricklefs et al., 1980 |
| Oceanodroma furcata | 44.6 | ? | ? | 39.2 | Vleck, Kenagu, 1980 |
| Oceanodroma furcata | 49.0 | ? | ? | 54.03 | Iversen, Krog, 1972 |
| Pelicanoides georgicus | 127 | S | N | 85 | Adams, Brown, 1984 |
| Pterodroma hypoleuca | 169 | W | D | 109.5 | Grant, Whittow, 1983 |
| Pterodroma brevirostris | 315 | S | N | 153 | Adams, Brown, 1984 |
| Pterodroma mollis | 274 | S | N | 151 | Adams, Brown, 1984 |
| Puffinus pacificus | 337.8 | ? | ? | 130.25 | Pettit, Ellis, Whittow (after Grant, Whittow, 1983) |
| Procellaria cinerea | 1014 | S | N | 433 | Adams, Brown, 1984 |
| Procellaria aequinoctialis | 1287 | S | N | 545 | Adams, Brown, 1984 |

| 1 | 2 | 3 | 4 | 5 | 6 |
|-----------------------------------|------|---|---|--------|----------------------------------|
| <i>Diomedea immutabilis</i> | 2522 | W | D | 645.5 | Grant, Whittow, 1983 |
| <i>Phoebastria fusca</i> | 2875 | S | N | 715 | Adams, Brown, 1984 |
| <i>Macronectes giganteus</i> ♀ | 3280 | S | N | 1418.3 | Ricklefs, Mattew, 1983 |
| <i>Macronectes giganteus</i> ♂ | 3980 | S | N | 1572.6 | Ricklefs, Mattew, 1983 |
| <i>Macronectes giganteus</i> | 4780 | S | N | 1154 | Adams, Brown, 1984 |
| <i>Diomedea chrysostoma</i> | 3753 | S | N | 735 | Adams, Brown, 1984 |
| <i>Diomedea exulans</i> | 8130 | S | N | 1755 | Adams, Brown, 1984 |
| <i>Pelecaniformes</i> | | | | | |
| <i>Fregata magnificus</i> | 1080 | ? | ? | 240.5 | Enger, 1957 |
| <i>Phalacrocorax atriceps</i> | 2600 | S | N | 1292.8 | Ricklefs, Mattew, 1983 |
| <i>Pelecanus occidentalis</i> | 3510 | ? | N | 1105.4 | Benedict, Fox, 1927 |
| <i>Pelecanus conspicillatus</i> | 5090 | ? | N | 1565.9 | Benedict, Fox, 1927 |
| <i>Ciconiiformes</i> | | | | | |
| <i>Botaurus leucomystax</i> | 600 | ? | N | 234.5 | Benedict, Fox, 1927 |
| <i>Guara alba</i> | 940 | ? | D | 355.9 | Benedict, Fox, 1927 |
| <i>Ardea herodias</i> | 1870 | ? | N | 536.0 | Benedict, Fox, 1927 |
| <i>Mycteria americana</i> | 2500 | ? | ? | 841.6 | Kahl, 1962 |
| <i>Phoenicopiterus antiquorum</i> | 3040 | ? | N | 900.2 | Benedict, Fox, 1927 |
| <i>Yabiru mycteria</i> | 5470 | ? | N | 1138.9 | Benedict, Fox, 1927 |
| <i>Leptoptilos javanicus</i> | 5710 | ? | N | 1285.4 | Benedict, Fox, 1927 |
| <i>Anseriformes</i> | | | | | |
| <i>Anas crecca</i> | 250 | ? | N | 144.0 | Prinzinger, Hänszler, 1980 |
| <i>Anas querquedula</i> | 289 | ? | N | 193.0 | Prinzinger, Hänszler, 1980 |
| <i>Aythya nyroca</i> | 440 | ? | N | 282.7 | Prinzinger, Hänszler, 1980 |
| <i>Aix sponsa</i> | 485 | ? | N | 261.3 | Herzog, 1930 |
| <i>Aix sponsa</i> | 485 | ? | D | 281.4 | Herzog, 1930 |
| <i>Anas penelope</i> | 539 | ? | N | 271.0 | Prinzinger, Hänszler, 1980 |
| <i>Anas clypeata</i> | 554 | ? | N | 335.0 | Prinzinger, Hänszler, 1980 |
| <i>Aythya fuligula</i> | 574 | ? | N | 233.5 | Prinzinger, Hänszler, 1980 |
| <i>Anas acuta</i> | 721 | ? | N | 377.0 | Prinzinger, Hänszler, 1980 |
| <i>Aythya ferina</i> | 816 | ? | N | 502.6 | Prinzinger, Hänszler, 1980 |
| <i>Anas platyrhynchos</i> | 1236 | ? | N | 654.7 | Prinzinger, Hänszler, 1980 |
| <i>Netta rufina</i> | 1237 | ? | N | 613.4 | Prinzinger, Hänszler, 1980 |
| <i>Branta bernicla</i> | 1130 | S | D | 454.3 | Irving et al., 1955 |
| <i>Branta bernicla</i> | 1168 | W | D | 391.1 | Irving et al., 1955 |
| <i>Branta bernicla</i> | 1379 | W | N | 718.1 | G. West (personal communication) |
| <i>Branta bernicla</i> | 1528 | S | N | 478.2 | G. West (personal communication) |
| Domestic duck | 1870 | ? | D | 657.4 | Giaja, Males, 1928 |
| <i>Anser canadica</i> ♀ | 2303 | ? | N | 780.5 | G. West (personal communication) |
| <i>Anser canadica</i> ♂ | 2915 | ? | N | 767.5 | G. West (personal communication) |
| <i>Anser canadica</i> | 2800 | S | N | 850.8 | West, Norton, 1976 |
| <i>Schauna chavaria</i> | 2620 | ? | N | 594.5 | Benedict, Fox, 1927 |

| 1 | 2 | 3 | 4 | 5 | 6 |
|----------------------------|-------|---|---|--------|----------------------------|
| Domestic goose | 3300 | ? | ? | 917.0 | Giaja, 1931 |
| Domestic goose | 5000 | ? | N | 1172.4 | Benedict, Lee, 1937 |
| Domestic goose ♀ | 5300 | ? | D | 1125.5 | Herzog, 1930 |
| Domestic goose ♀ | 5450 | ? | N | 1095.3 | Herzog, 1930 |
| Domestic goose ♂ | 6050 | ? | D | 1256.1 | Herzog, 1930 |
| Domestic goose ♂ | 6300 | ? | N | 1065.2 | Herzog, 1930 |
| Cygnus buccinator | 8800 | ? | N | 1750.2 | Benedict, Fox, 1927 |
| Falconiformes | | | | | |
| Falco tinnunculus | 108 | ? | D | 71.2 | Giaja, Males, 1928 |
| Falco sparverius | 104.7 | W | N | 51.2 | Gatehouse, Markham, 1970 |
| Falco sparverius | 104.7 | W | D | 88.7 | Gatehouse, Markham, 1970 |
| Falco sparverius ♂ | 117.7 | ? | N | 72.9 | Shapiro, Weathers, 1981 |
| Buteo buteo | 1012 | ? | N | 324.5 | Prinzinger, Hänssler, 1980 |
| Cathartes aura | 1100 | ? | ? | 247.3 | Enger, 1957 |
| Coragyps atratus | 1700 | ? | ? | 383.0 | Enger, 1957 |
| Geranoaëtus melanoleucus | 2860 | ? | N | 443.8 | Benedict, Fox, 1927 |
| Aquila chrysaëtos | 3000 | ? | D | 427.1 | Giaja, Males, 1928 |
| Gypaëtus barbatus | 5070 | ? | N | 954.6 | Benedict, Fox, 1927 |
| Vultur gryphus | 10320 | ? | N | 1469.6 | Benedict, Fox, 1927 |
| Galliformes | | | | | |
| Excalfactoria chinensis | 42.7 | ? | ? | 25.1 | Lasiewski, Dawson, 1967 |
| Excalfactoria chinensis | 49 | ? | N | 54.2 | Prinzinger, Hänssler, 1980 |
| Coturnix coturnix | 97 | ? | D | 96.3 | Giaja, Males, 1928 |
| Coturnix coturnix japonica | 100.6 | S | N | 92.1 | Weathers, 1981 |
| Coturnix coturnix japonica | 115 | ? | N | 84.5 | Prinzinger, Hänssler, 1980 |
| Lophortyx gambelii | 125.5 | S | N | 65.0 | Weathers, 1981 |
| Lophortyx californicus | 137.1 | ? | ? | 67.0 | Hudson, Brush, 1964 |
| Colinus virginianus | 194 | ? | ? | 96.3 | Lasiewski, Dawson, 1967 |
| Alectoris chukar | 475 | S | ? | 169.5 | Marder, Bernstein, 1983 |
| Domestic fowl | 865 | ? | N | 242.0 | Terroine et al., 1926 |
| Domestic fowl | 865 | ? | D | 296.4 | Terroine et al., 1926 |
| Domestic fowl | 1600 | ? | N | 417.0 | Herzog, 1930 |
| Domestic fowl | 1600 | ? | D | 512.5 | Herzog, 1930 |
| Domestic fowl | 1800 | ? | N | 427.1 | Bacq, 1929 |
| Domestic fowl | 1800 | ? | D | 633.1 | Bacq, 1929 |
| Domestic fowl | 2000 | ? | N | 408.2 | Benedict, 1938 |
| Domestic fowl | 2000 | ? | D | 481.5 | Duckes, 1937 |
| Domestic fowl | 2200 | ? | N | 542.6 | Barott, Pringle, 1941 |
| Domestic fowl | 2200 | ? | D | 713.5 | Barott, Pringle, 1941 |
| Domestic fowl | 2270 | ? | N | 718.5 | Herzog, 1930 |
| Domestic fowl | 2270 | ? | D | 964.7 | Herzog, 1930 |
| Domestic fowl | 2710 | ? | N | 519.2 | Winchester, 1940 |
| Penelope purpurensis | 2040 | ? | N | 468.9 | Benedict, Fox, 1927 |

| 1 | 2 | 3 | 4 | 5 | 6 |
|---------------------------------|--------|---|---|--------|----------------------------|
| <i>Grax alberti</i> | 2800 | ? | N | 569.4 | Benedict, Fox, 1927 |
| Domestic turkey | 3700 | ? | ? | 770.4 | Giaja, 1931 |
| <u>Gruiformes</u> | | | | | |
| <i>Fulica atra</i> | 754 | ? | N | 377.0 | Prinzinger, Hänssler, 1980 |
| <i>Grus canadensis</i> | 3890 | ? | D | 703.4 | Benedict, Fox, 1927 |
| <i>Antropoides paradisea</i> | 4030 | ? | N | 921.1 | Benedict, Fox, 1927 |
| <u>Charadriiformes</u> | | | | | |
| <i>Tringa ochropus</i> | 90 | ? | N | 79.7 | Prinzinger, Hänssler, 1980 |
| <i>Catharacta skua</i> | 970 | ? | D | 410.3 | Benedict, Fox, 1927 |
| <i>Stercorarius maccormicki</i> | 1130 | S | N | 742.9 | Ricklefs, Matthew, 1983 |
| <i>Gabianus pacificus</i> | 1210 | ? | D | 531.7 | Benedict, Fox, 1927 |
| <i>Uria lomvia</i> | (1300) | ? | ? | 587.8 | Johnson, West, 1975 |
| <i>Uria aalge</i> | (1300) | ? | ? | 587.8 | Johnson, West, 1975 |
| <i>Larus hyperborues</i> | 1600 | ? | D | 1278.8 | Scholander et al., 1950 |
| <u>Columbiformes</u> | | | | | |
| <i>Scardafella inca</i> | 40.5 | ? | ? | 21.8 | MacMillen, Trost, 1965 |
| <i>Zenaidura macroura</i> | 123 | ? | N | 63.6 | Riddle et al., 1932 |
| <i>Leptoptila vereauxi</i> | 131 | A | N | 76.6 | Vleck, Vleck, 1979 |
| <i>Columba palumbus</i> | 150 | ? | N | 71.2 | Benedict, 1938 |
| <i>Streptopelia risoria</i> | 150 | ? | N | 76.2 | Benedict, Riddle, 1928 |
| <i>Streptopelia risoria</i> | 150 | ? | D | 91.3 | Benedict, Riddle, 1928 |
| <i>Streptopelia decaocto</i> | 152 | ? | D | 91.3 | Giaja, Males, 1928 |
| <i>Streptopelia decaocto</i> | 155 | ? | D | 76.6 | Gelineo, 1955 |
| <i>Streptopelia decaocto</i> | 161 | V | N | 72.8 | Gavrilov (unpublished) |
| <i>Columba livia</i> | 250 | S | N | 108.1 | Riddle et al., 1932 |
| <i>Columba livia</i> | 280 | W | N | 114.8 | Riddle et al., 1932 |
| <i>Columba livia</i> | 266 | ? | D | 141.1 | Gelineo, 1955 |
| <i>Columba livia</i> | 275 | ? | N | 136.5 | Terroine et al., 1926 |
| <i>Columba livia</i> | 275 | ? | D | 188.8 | Terroine et al., 1926 |
| <i>Columba livia</i> | 300 | ? | N | 143.6 | Benedict, Riddle, 1928 |
| <i>Columba livia</i> | 300 | ? | D | 154.9 | Benedict, Riddle, 1928 |
| <i>Columba livia</i> | 300 | ? | N | 130.6 | Burckard et al., 1934 |
| <i>Columba livia</i> | 300 | ? | D | 163.7 | Burckard et al., 1934 |
| <i>Columba livia</i> | 300 | ? | N | 125.6 | Benedict, 1938 |
| <i>Columba livia</i> | 311 | ? | N | 137.7 | Burckard et al., 1933 |
| <i>Columba livia</i> | 320 | ? | N | 110.5 | Kayser, 1929 |
| <i>Columba livia</i> | 320 | ? | D | 133.6 | Kayser, 1929 |
| <i>Columba livia</i> | 330 | ? | N | 123.5 | Dontcheff et al., 1935 |
| <i>Columba livia</i> | 330 | ? | D | 148.6 | Dontcheff et al., 1935 |
| <i>Columba livia</i> | 370 | ? | N | 156.6 | Herzog, 1930 |
| <i>Columba livia</i> | 370 | ? | D | 190.1 | Herzog, 1930 |
| <i>Columba livia</i> | 381 | S | N | 253.9 | Hart, 1962 |
| <i>Columba livia</i> | 405 | W | N | 239.9 | Hart, 1962 |

| 1 | 2 | 3 | 4 | 5 | 6 |
|--------------------------------|-------|---|------|-------|------------------------------|
| <u>Psittaciformes</u> | | | | | |
| <i>Loriculus galgulus</i> | 27 | ? | N | 44.6 | Prinzinger, Hänsler, 1980 |
| <i>Melopsittacus undulatus</i> | 33.7 | W | D | 41.5 | Weathers, Schoenbaeher, 1976 |
| <i>Melopsittacus undulatus</i> | 39 | ? | N | 70.6 | Prinzinger, Hänsler, 1980 |
| <i>Neophema pulchella</i> | 40 | ? | N | 50.2 | Prinzinger, Hänsler, 1980 |
| <i>Neophema bourkii</i> | 40 | ? | N | 49.6 | Prinzinger, Hänsler, 1980 |
| <i>Myiopsitta monachus</i> | 80.4 | W | N | 45.4 | Weathers, Caccamise, 1975 |
| <i>Myiopsitta monachus</i> | 83.1 | S | N | 60.1 | Weathers, Caccamise, 1978 |
| <u>Cuculiformes</u> | | | | | |
| <i>Cacomantis variolus</i> | 23.8 | W | N | 10.5 | Hails, 1983 |
| <i>Cacomantis variolus</i> | 23.8 | W | D | 16.4 | Hails, 1983 |
| <i>Cuculus canorus</i> | 128 | ? | N | 108.5 | Prinzinger, Hänsler, 1980 |
| <i>Centropus senegalensis</i> | 175 | ? | N | 130.3 | Prinzinger, Hänsler, 1980 |
| <i>Eudynamis scolopacea</i> | 188 | ? | N | 142.1 | Prinzinger, Hänsler, 1980 |
| <u>Strigiformes</u> | | | | | |
| <i>Glaucidium gnome</i> | 54 | S | D | 39.0 | Ligon, 1969 |
| <i>Otus scops</i> | 63.9 | W | N | 30.6 | Hails, 1983 |
| <i>Otus scops</i> | 78.9 | S | D | 40.8 | Gavrilov(unpublished) |
| <i>Otus scops</i> | 80.4 | W | D | 44.3 | Gavrilov(unpublished) |
| <i>Aegolius acadicus</i> | 82.9 | W | N | 71.3 | Gatehouse, Markham, 1970 |
| <i>Aegolius acadicus</i> | 82.9 | W | D | 44.4 | Gatehouse, Markham, 1970 |
| <i>Aegolius acadicus</i> | 85.5 | W | ? | 60.7 | Graber, 1962 |
| <i>Aegolius acadicus</i> | 105.5 | ? | ? | 67.8 | Collins, 1963 |
| <i>Aegolius acadicus</i> | 124 | S | D | 57.0 | Ligon, 1969 |
| <i>Otus trichopsis</i> | 120 | S | D | 38.0 | Ligon, 1969 |
| <i>Otus asio</i> | 151.4 | W | N | 97.1 | Gatehouse, Markham, 1970 |
| <i>Otus asio</i> | 151.4 | W | D | 61.3 | Gatehouse, Markham, 1970 |
| <i>Otus asio</i> | 166 | S | D | 51.0 | Ligon, 1969 |
| <i>Glaucidium cuculoides</i> | 163 | S | ? | 75.0 | Johnson, Collins, 1975 |
| <i>Asio otus</i> | 241 | Y | N, D | 114.0 | Wijnandts, 1984 |
| <i>Asio otus</i> | 252 | ? | N | 89.6 | Graber, 1962 |
| <i>Asio otus</i> | 252 | ? | D | 137.7 | Graber, 1962 |
| <i>Surnua ulula</i> | 333 | W | ? | 147.0 | Johnson, Collins, 1975 |
| <i>Asio flammeus</i> | 406 | ? | N | 148.6 | Graber, 1962 |
| <i>Asio flammeus</i> | 406 | ? | D | 177.9 | Graber, 1962 |
| <i>Strix aluco</i> | 520 | ? | N | 180.0 | Herzog, 1930 |
| <i>Bubo virginianus</i> | 1450 | ? | D | 452.2 | Benedict, Fox, 1927 |

| 1 | 2 | 3 | 4 | 5 | 6 |
|----------------------------------|------|---|---|------|----------------------------|
| <u>Caprimulgiiformes</u> | | | | | |
| <i>Nictidromus albicollis</i> | 43 | ? | D | 39.8 | Scholander et al., 1950 |
| <i>Eurostopodus guttatus</i> | 88 | ? | ? | 35.2 | Dawson, Fisher, 1969 |
| <u>Apodiiformes</u> | | | | | |
| <i>Stellula ealliope</i> | 3.0 | ? | D | 5.7 | Lasiewski, 1963 |
| <u>Coliiformes</u> | | | | | |
| <i>Urocolius macrourus</i> | 48.5 | ? | N | 63.7 | Hoffmann, Prinzinger, 1984 |
| <i>Colius striatus</i> | 51.2 | ? | N | 47.0 | Hoffman, Prinzinger, 1984 |
| <i>Colius striatus</i> | 52.5 | ? | N | 26.8 | Bartholomew, Trost, 1970 |
| <i>Urocolius indicus</i> | 53.5 | ? | N | 61.9 | Hoffmann, Prinzinger, 1984 |
| <i>Colius eastanotus</i> | 57.7 | ? | N | 66.1 | Hoffmann, Prinzinger, 1984 |
| <u>Coraciiformes</u> | | | | | |
| <i>Upupa epops</i> | 67 | ? | N | 47.8 | Prinzinger, Hänsler, 1980 |
| <u>Passeriformes</u> | | | | | |
| <i>Acrocephalus bistrigiceps</i> | 7.9 | W | N | 11.1 | Hails, 1983 |
| <i>Uraeginthus bengelis</i> | 8.1 | ? | ? | 11.7 | Lasiewski et al., 1964 |
| <i>Phylloscopus trochilus</i> | 8.5 | ? | N | 16.7 | Aschoff, Pohl, 1970 |
| <i>Phylloscopus trochilus</i> | 8.5 | ? | D | 20.1 | Aschoff, Pohl, 1970 |
| <i>Lonchura malabarica</i> | 10.6 | ? | D | 17.6 | Willoughby, 1969 |
| <i>Hypothymis azurea</i> | 10.8 | W | N | 12.0 | Hails, 1983 |
| <i>Hypothymis azurea</i> | 10.8 | W | D | 15.3 | Hails, 1983 |
| <i>Acanthis flammea</i> | 11.2 | ? | N | 24.3 | Steen, 1958 |
| <i>Amphispiza bilineata</i> | 11.6 | S | N | 17.3 | Weathers, 1981 |
| <i>Lonchura malacca</i> | 11.8 | W | N | 12.2 | Hails, 1983 |
| <i>Lonchura malacca</i> | 11.8 | W | D | 19.1 | Hails, 1983 |
| <i>Pipra mentalis</i> | 12.0 | ? | D | 27.2 | Scholander et al., 1950 |
| <i>Pipra mentalis</i> | 12.3 | S | D | 22.2 | Bartholomew et al., 1983 |
| <i>Pipra mentalis</i> | 14.5 | A | N | 25.7 | Vleck, Vleck, 1979 |
| <i>Lonchura maja</i> | 12.8 | W | N | 13.2 | Hails, 1983 |
| <i>Lonchura maja</i> | 12.8 | W | D | 23.2 | Hails, 1983 |
| <i>Arachnotera longirosta</i> | 13.0 | W | N | 16.3 | Hails, 1983 |
| <i>Arachnotera longirosta</i> | 13.0 | W | D | 21.0 | Hails, 1983 |
| <i>Spinus spinus</i> | 13.0 | ? | D | 24.3 | Gelineo, 1955 |
| <i>Erithacus cyane</i> | 13.4 | W | N | 15.0 | Hails, 1983 |
| <i>Erithacus cyane</i> | 13.4 | W | D | 22.9 | Hails, 1983 |
| <i>Spinus pinus</i> | 13.8 | W | N | 30.1 | Dawson, Carey, 1976 |
| <i>Himatione sanguinea</i> | 13.8 | ? | D | 23.2 | MacMillen, Carpenter, 1977 |
| <i>Himatione sanguinea</i> | 15.5 | W | N | 29.2 | Weathers et al., 1983 |
| <i>Himatione sanguinea</i> | 19.5 | W | N | 37.3 | Weathers et al., 1983 |
| <i>Serinus canaria</i> | 15.0 | ? | N | 19.3 | Benedict, Fox, 1933 |
| <i>Serinus canaria</i> | 15.0 | ? | D | 23.0 | Benedict, Fox, 1933 |

| 1 | 2 | 3 | 4 | 5 | 6 |
|----------------------------------|------|---|---|------|----------------------------|
| <i>Serinus canaria</i> | 15.6 | S | D | 26.6 | Gelineo, 1969 |
| <i>Serinus canaria</i> | 15.8 | W | D | 38.4 | Gelineo, 1969 |
| <i>Manacus vitellinus</i> ♀ | 15.0 | A | N | 24.7 | Vleck, Vleck, 1979 |
| <i>Manacus vitellinus</i> ♂ | 18.2 | A | N | 20.4 | Vleck, Vleck, 1979 |
| <i>Manacus vitellinus</i> | 15.5 | S | D | 20.7 | Bartholomew et al., 1983 |
| <i>Acanthis cannabina</i> | 15.5 | ? | D | 30.6 | Gelineo, 1955 |
| <i>Malacopteron cinereum</i> | 15.8 | W | N | 18.3 | Hails, 1983 |
| <i>Malacopteron cinereum</i> | 15.8 | W | D | 27.1 | Hails, 1983 |
| <i>Carduelis carduelis</i> | 16.7 | S | D | 28.4 | Gelineo, 1969 |
| <i>Carduelis carduelis</i> | 16.6 | W | D | 35.8 | Gelineo, 1969 |
| <i>Vestiaria coccinea</i> | 16.9 | S | D | 30.1 | MacMillen, Carpenter, 1977 |
| <i>Spizella arborea</i> | 16.6 | ? | ? | 28.5 | Losiewski, Dawson, 1967 |
| <i>Passer montanus</i> | 17.5 | W | N | 17.1 | Hails, 1983 |
| <i>Passer montanus</i> | 17.5 | W | D | 28.6 | Hails, 1983 |
| <i>Passer montanus</i> | 22.0 | ? | N | 35.6 | Steen, 1958 |
| <i>Delichon urbica</i> | 17.8 | S | N | 19.4 | Hails, 1983 |
| <i>Junco hyemalis</i> | 18.0 | ? | ? | 25.5 | Lasiewski, Dawson, 1967 |
| <i>Parus major</i> | 18.5 | ? | N | 35.2 | Steen, 1958 |
| <i>Melospiza melodia</i> | 18.6 | ? | ? | 32.7 | Lasiewski, Dawson, 1967 |
| <i>Carpodacus mexicanus</i> | 20.4 | S | N | 26.8 | Weathers, 1981 |
| <i>Thamnophilus punctatus</i> | 21.0 | A | N | 29.5 | Vleck, Vleck, 1979 |
| <i>Fringilla montifringilla</i> | 21.0 | ? | N | 33.1 | Aschoff, Pohl, 1970 |
| <i>Fringilla montifringilla</i> | 21.0 | ? | D | 46.1 | Aschoff, Pohl, 1970 |
| <i>Fringilla montifringilla</i> | 24.8 | ? | N | 39.8 | Steen, 1958 |
| <i>Acrocephalus arundinaceus</i> | 21.9 | W | N | 22.0 | Hails, 1983 |
| <i>Acrocephalus arundinaceus</i> | 21.9 | W | D | 26.0 | Hails, 1983 |
| <i>Fringilla coelebs</i> | 22.0 | ? | N | 31.0 | Pohl, 1969 |
| <i>Fringilla coelebs</i> | 22.0 | ? | D | 40.2 | Pohl, 1969 |
| <i>Zonotrichia albicollis</i> | 22.5 | ? | D | 47.3 | Hudson, Kimzey, 1964 |
| <i>Zonotrichia albicollis</i> | 23.6 | ? | ? | 39.8 | Lasiewski, Dawson, 1967 |
| <i>Passer domesticus</i> | 22.4 | W | N | 39.8 | Fonberg, 1932 |
| <i>Passer domesticus</i> | 22.9 | ? | D | 43.1 | Quirring, Bade, 1943 |
| <i>Passer domesticus</i> | 23.5 | V | N | 46.1 | Fonberg, 1932 |
| <i>Passer domesticus</i> | 25.0 | ? | N | 28.9 | Miller, 1939 |
| <i>Passer domesticus</i> | 25.4 | ? | D | 45.2 | Hudson, Kimzey, 1966 |
| <i>Passer domesticus</i> | 25.5 | ? | D | 39.4 | Hudson, Kimzey, 1964 |
| <i>Passer domesticus</i> | 26.0 | ? | D | 39.4 | Gelineo, 1955 |
| <i>Passer domesticus</i> | 27.1 | S | ? | 58.1 | Hart, 1962 |
| <i>Passer domesticus</i> | 27.3 | ? | N | 35.6 | Steen, 1958 |
| <i>Passer domesticus</i> | 28.2 | S | ? | 51.7 | Palokangas et al., 1975 |
| <i>Passer domesticus</i> | 29.4 | W | ? | 77.1 | Hart, 1962 |
| <i>Carduelis chloris</i> | 24.5 | ? | D | 46.5 | Gelineo, 1955 |
| <i>Carduelis chloris</i> | 31.1 | ? | N | 46.9 | Steen, 1958 |
| <i>Zonotrichia leucophrys</i> | 25.5 | W | N | 41.3 | Southwick, 1980 |
| <i>Zonotrichia leucophrys</i> | 27.0 | S | N | 32.6 | Southwick, 1980 |
| <i>Carpodacus cassinii</i> | 26.8 | S | N | 28.7 | Weathers, 1981 |

| 1 | 2 | 3 | 4 | 5 | 6 |
|-------------------------|--------|---|---|-------|-------------------------|
| Lanius cristatus | 26.9 | W | N | 21.8 | Hails, 1983 |
| Lanius cristatus | 26.9 | W | D | 26.3 | Hails, 1983 |
| Pycnonotus finlaysoni | 26.3 | W | N | 19.4 | Hails, 1983 |
| Pycnonotus finlaysoni | 26.3 | W | D | 27.1 | Hails, 1983 |
| Pycnonotus goiavier | 28.6 | W | N | 21.1 | Hails, 1983 |
| Pycnonotus goiavier | 28.6 | W | D | 29.3 | Hails, 1983 |
| Passerella illiaca | 31.7 | ? | ? | 47.3 | Lasiewski, Dawson, 1967 |
| Calamospiza melanocoryx | 33.0 | ? | ? | 38.0 | Wunder, 1979 |
| Copsychus saularis | 33.5 | W | N | 20.0 | Hails, 1983 |
| Copsychus saularis | 33.5 | W | D | 29.0 | Hails, 1983 |
| Molothrus ater | 33.7 | ? | ? | 46.1 | Lasiewski, Dawson, 1967 |
| Criniger bres | 35.0 | W | N | 30.7 | Hails, 1983 |
| Criniger bres | 35.0 | W | D | 40.1 | Hails, 1983 |
| Arachnotera flavigaster | 36.3 | W | N | 25.8 | Hails, 1983 |
| Icterus bullockii | (37.5) | S | N | 42.2 | Rising, 1969 |
| Icterus galbula | (37.5) | S | N | 42.2 | Rising, 1969 |
| Arachnotera flavigaster | 36.3 | W | N | 35.3 | Hails, 1983 |
| Chloropsis sonnerati | 39.7 | W | N | 32.7 | Hails, 1983 |
| Plectrophenax nivalis | 41.8 | ? | D | 47.7 | Scholander et al., 1950 |
| Xiphorhynchus guttatus | 45.2 | A | N | 38.6 | Vleck, Vleck, 1979 |
| Agelaeus phoeniceus | 46.3 | S | N | 44.8 | Weathers, 1981 |
| Perisoreus canadensis | 64.5 | ? | D | 83.7 | Scholander et al., 1950 |
| Sturnus vulgaris | 68.0 | ? | ? | 74.1 | Brenner, 1962 |
| Sturnus vulgaris | 79.6 | S | ? | 145.6 | Hart, 1962 |
| Sturnus vulgaris | 86.8 | W | ? | 158.7 | Hart, 1962 |
| Nucifraga caryocatactes | 165.0 | ? | N | 126.4 | Aschoff, Pohl, 1970 |
| Nucifraga caryocatactes | 165.0 | ? | D | 129.8 | Aschoff, Pohl, 1970 |
| Pyrrhocorax graculus | 177.0 | ? | N | 129.8 | Aschoff, Pohl, 1970 |
| Pyrrhocorax graculus | 177.0 | ? | D | 168.7 | Aschoff, Pohl, 1970 |
| Pica pica | 193.0 | ? | N | 134.0 | Aschoff, Pohl, 1970 |
| Pica pica | 193.0 | ? | D | 172.9 | Aschoff, Pohl, 1970 |
| Corvus caurinus | 282.0 | S | ? | 306.5 | Irving et al., 1955 |
| Corvus caurinus | 306.0 | W | ? | 404.9 | Irving et al., 1955 |
| Corvus corone | 515 | ? | N | 335.8 | Aschoff, Pohl, 1970 |
| Corvus corone | 515 | ? | D | 404.9 | Aschoff, Pohl, 1970 |
| Corvus ruficollis | 610 | S | D | 292.8 | Marder, 1973 |
| Corvus ruficollis | 640 | S | N | 276.3 | Gavrilov, 1979 |
| Corvus cryptoleucus | 640 | ? | ? | 330.8 | Lasiewski, Dawson, 1967 |
| Corvus corax | 850 | ? | D | 385.2 | Scholander et al., 1950 |
| Corvus corax | 866 | ? | ? | 397.3 | Lasiewski, Dawson, 1967 |
| Corvus corax | 975 | S | ? | 716.3 | Veghte, 1975 |
| Corvus corax | 1069 | W | ? | 785.4 | Veghte, 1975 |

III. EXISTENCE ENERGY IN BIRDS

Existence metabolism is the rate at which energy is used by caged birds for maintenance of their living in absence of reproduction, moult, migratory unrest, growth, or changes in the early morning body mass. EM is determined by subtracting of the daily excretory energy from daily gross energy intake in birds maintaining a constant body mass over a period of several days. The experimental cage volume should be enough for the realization of the most of energy expended locomotions in experimental birds, including walking, running, hopping and very short-distance flights. EM is equal to daily energy expenditure in free-living birds on the energy value more than all others energetical indices measured in laboratory.

The existence metabolism rate is inversely correlated to ambient temperatures. This correlation can be approximated by linear regression (Fig. 2). Slope of this regression is the temperature coefficient of EM (h_{EM}). The temperature coefficient of EM predict better thermoregulatory heat production in free-living birds than the standard metabolic rate temperature coefficient because of h_{EM} is an integration of heat increment of feeding, heat production by locomotions, heat production for temperature regulation and effects of measuring of thermoconductive properties in various postures, daily changes of BM rate and changes of the body temperature under different ambient temperatures.

The existence metabolic rate of a given avian species may be presented in a standard form as EM at two standard ambient temperatures (0°C and 30°C). EM_0 and EM_{30} are calculated from species-specific regression of EM rate relation to T_a .

30°C was selected because this temperature is thermoneutral for most species of birds. EM_{30} is therefore the cost of existence without energy expenditure for thermoregulation.

0°C was selected because this temperature is lower than the lower critical temperature in most species of birds. EM_0 incorporates therefore the cost of existence and the cost of thermoregulation.

EM_{T_a} of a given bird at given T_a can be obtained from regression:

$$EM_{T_a} = EM_0 - h_{EM} T_a$$

The right part of the regression is presented in Table 3 for every species. In addition EM_{30} is presented for every species. The table contains 275 data on the existence metabolic rate in various species, collected from the world publications. This check-list contains 14% new data in comparison with the check-list of Kendeigh et al. (1977).

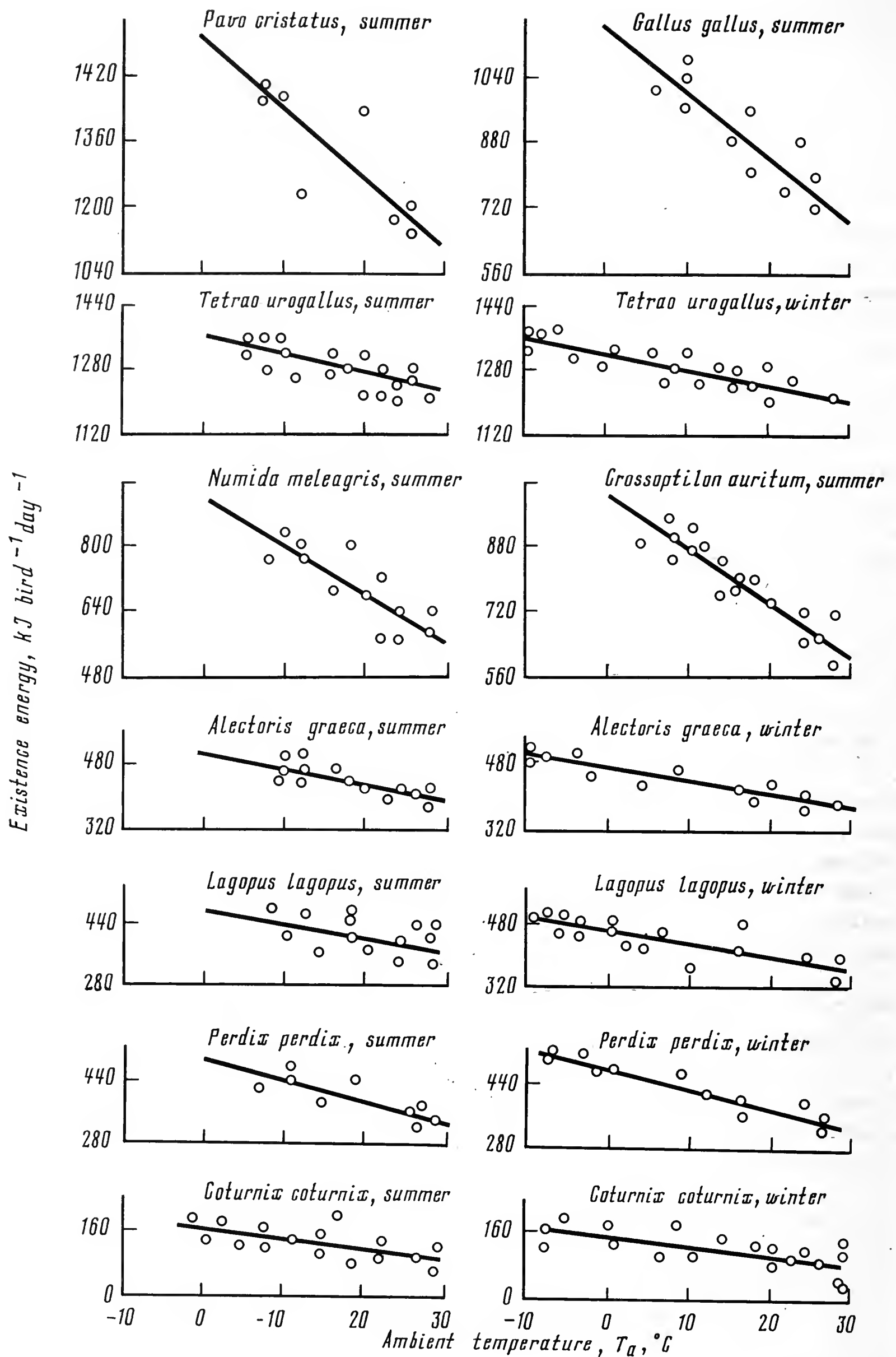


Fig. 2. Example of relation of existence energy on ambient temperature in some species of Galliformes (after Gavrilov, 1980)

T a b l e 3. Existence metabolic rate in bird

| Species | Body mass, g | Season | $EM_{O^{\circ}}$ kJ bird ⁻¹ day ⁻¹ | h_{EM} kJ bird ⁻¹ day ⁻¹ °C ⁻¹ | $EM_{30^{\circ}}$ kJ bird ⁻¹ day ⁻¹ | References |
|----------------------------|--------------|--------|---|--|--|-------------------------------|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| <u>Sphenisciformes</u> | | | | | | |
| Edyptes cristatus | 2330 | (W) | 1040.0 | 11.21 | 703.7 | Gavrilov, 1977 |
| Eudytes chrysolophus | 3860 | (W) | 1525.3 | 10.47 | 1211.3 | Gavrilov, 1977 |
| Aptenodytes patagonica | 11080 | (W) | 2529.9 | 8.67 | 2269.8 | Gavrilov, 1977 |
| <u>Struthioniformes</u> | | | | | | |
| Struthio camelus | 122000 | S | 11672.1 | 21.26 | 11023.0 | Gavrilov, Dolnik(unpublished) |
| <u>Rheiformes</u> | | | | | | |
| Rhea americana | 32000 | S | 4841.8 | 8.01 | 4601.5 | Gavrilov, Dolnik(unpublished) |
| <u>Casuariiformes</u> | | | | | | |
| Dromiceus novae-hollandiae | 45000 | S | 6123.4 | 8.97 | 5857.2 | Gavrilov, Dolnik(unpublished) |
| Caruaris casuaris | 52000 | S | 6717.2 | 16.33 | 6227.3 | Gavrilov, Dolnik(unpublished) |
| <u>Ciconiiformes</u> | | | | | | |
| Botaurus stellaris | 1010 | S | 772.5 | 12.03 | 411.6 | Gavrilov, Dolnik(unpublished) |
| Phoenicopterus roseus | 3980 | S | 1621.6 | 16.75 | 1119.2 | Gavrilov, Dolnik(unpublished) |
| Leptoptilus cruminiferus | 5760 | S | 1877.5 | 16.55 | 1380.9 | Gavrilov, Dolnik(unpublished) |
| Gabirus mycteria | 6020 | | 1894.2 | 14.49 | 1459.6 | Gavrilov, Dolnik(unpublished) |
| <u>Anseriformes</u> | | | | | | |
| Anas discors (♀) | 309 | W | 447.6 | 8.17 | 202.4 | Owen, 1970 |
| Anas discors (♂) | 363 | W | 489.4 | 9.26 | 211.2 | Owen, 1970 |
| Aix sponsa | 448 | S | 467.7 | 7.38 | 246.2 | Gavrilov (in press) |
| Aix sponsa | 448 | W | 470.6 | 7.37 | 249.5 | Gavrilov (in press) |
| Dendrocygna autumnalis | 707 | S | 664.1 | 7.22 | 447.5 | Cain, 1973 |
| Dendrocygna autumnalis | 707 | W | 801.0 | 13.77 | 387.9 | Cain, 1973 |
| Anas penelope | 723 | S | 664.1 | 7.22 | 447.5 | Gavrilov (in press) |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|----------------------------|------|---|--------|-------|--------|--------------------------------|
| Anas penelope | 723 | W | 584.9 | 6.50 | 389.9 | Gavrilov (in press) |
| Netta frufina | 1020 | S | 562.3 | 3.00 | 472.3 | Gavrilov, Dolnik (unpublished) |
| Anas platyrhynchos | 1070 | S | 773.3 | 9.58 | 486.1 | Gavrilov (in press) |
| Anas platyrhynchos | 1070 | W | 689.2 | 8.45 | 435.8 | Gavrilov (in press) |
| Branta ruficollis | 1120 | S | 750.7 | 8.37 | 499.6 | Gavrilov, Dolnik (unpublished) |
| Chloephaga leucopterus | 2725 | S | 1334.8 | 11.23 | 997.8 | Gavrilov, Dolnik (unpublished) |
| Anser anser | 3250 | S | 1474.2 | 11.61 | 1125.9 | Gavrilov (in press) |
| Anser anser | 3400 | W | 1311.9 | 10.45 | 998.4 | Gavrilov (in press) |
| Branta canadensis | 4300 | S | 2158.4 | 19.15 | 1583.9 | Williams, 1965 |
| Branta canadensis | 4300 | W | 2121.1 | 22.58 | 1443.8 | Williams, 1965 |
| Cereopsis novae-hollandiae | 4500 | W | 1609.9 | 13.68 | 1199.5 | Gavrilov, Dolnik (unpublished) |
| <u>Falconiformes</u> | | | | | | |
| Accipiter nisus | 149 | A | 248.3 | 4.06 | 126.4 | Gavrilov, Dolnik (unpublished) |
| Pernis aprivorus | 649 | S | 583.7 | 8.47 | 329.6 | Gavrilov, Dolnik (unpublished) |
| Buteo buteo | 983 | S | 670.8 | 7.09 | 458.1 | Gavrilov, Dolnik (unpublished) |
| Neophron perenopterus | 2063 | S | 1174.0 | 15.37 | 713.0 | Gavrikov, Dolnik (unpublished) |
| Sarcoramphus papa | 3650 | S | 1472.6 | 14.42 | 1040.1 | Gavrilov, Dolnik (unpublished) |
| Harpia harpyja | 4300 | W | 1755.7 | 15.44 | 1292.5 | Gavrilov, Dolnik (unpublished) |
| <u>Galliformes</u> | | | | | | |
| Exalfactoria chinensis | 39 | S | 141.5 | 3.03 | 50.7 | Gavrilov, 1980 |
| Exalfactoria chinensis | 41 | W | 131.0 | 2.85 | 45.5 | Gavrilov, 1980 |
| Coturnix coturnix | 97 | S | 177.1 | 2.68 | 96.7 | Gavrilov, 1980 |
| Coturnix coturnix | 97 | W | 157.4 | 2.18 | 92.1 | Gavrilov, 1980 |
| Colinus virginianus | 189 | S | 291.2 | 8.16 | 46.1 | Cose, Robel, 1974 |
| Colinus virginianus | 189 | W | 205.2 | 3.52 | 99.6 | Case, Robel, 1974 |
| Perdix perdix | 483 | S | 470.6 | 5.24 | 313.4 | Gavrilov, 1980 |
| Perdix perdix | 483 | W | 455.1 | 4.49 | 320.3 | Gavrilov, 1980 |
| Lagopus lagopus | 524 | S | 440.9 | 3.34 | 340.8 | Gavrilov, 1980 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---------------------------|------|---|--------|-------|--------|-------------------------------------|
| Lagopus lagopus | 524 | W | 466.4 | 3.40 | 364.6 | Gavrilov, 1980 |
| Alectoris graeca | 620 | S | 487.4 | 3.90 | 370.3 | Gavrilov, 1980 |
| Alectoris graeca | 620 | W | 466.0 | 3.50 | 360.9 | Moore, 1961 |
| Phasianus versicolor (♀) | 800 | S | 670.3 | 11.08 | 338.0 | Moore, 1961 |
| Phasianus versicolor (♀) | 800 | W | 489.0 | 7.67 | 259.0 | Moore, 1961 |
| Phasianus versicolor (♂) | 1000 | S | 759.9 | 10.29 | 451.3 | Moore, 1961 |
| Phasianus versicolor (♂) | 1000 | W | 722.3 | 11.46 | 378.3 | Moore, 1961 |
| Phasianus colchicus (♀) | 800 | S | 548.9 | 8.25 | 327.3 | H.C.Seibert (Kendeigh et al., 1977) |
| Phasianus colchicus (♀) | 800 | W | 441.3 | 2.65 | 361.9 | H.C.Seibert (Kendeigh et al., 1977) |
| Phasianus colchicus (♂) | 1400 | S | 681.1 | 9.16 | 407.3 | H.C.Seibert (Kendeigh et al., 1977) |
| Phasianus colchicus (♂) | 1400 | W | 598.7 | 2.37 | 527.5 | H.C.Seibert (Kendeigh et al., 1977) |
| Symaticus reevesii (♀) | 1000 | S | 636.4 | 10.74 | 314.2 | Seibert, 1963 |
| Symaticus reevesii (♀) | 1000 | W | 551.9 | 4.75 | 404.4 | Seibert, 1963 |
| Symaticus reevesii (♂) | 1300 | S | 863.8 | 10.40 | 551.8 | Seibert, 1963 |
| Symaticus reevesii (♂) | 1300 | W | 861.7 | 10.79 | 538.1 | Seibert, 1963 |
| Crossoptilon crossoptilon | 1560 | S | 993.6 | 12.35 | 623.0 | Gavrilov, 1980 |
| Crossoptilon auritum | 1580 | S | 1051.8 | 13.79 | 638.1 | Gavrilov, 1980 |
| Numida meleagris | 1610 | S | 968.5 | 12.56 | 591.6 | Gavrilov, 1980 |
| Gallus gallus | 2330 | S | 1208.8 | 16.37 | 832.0 | Gavrilov, 1980 |
| Tetrao urogallus (♀) | 3900 | S | 1424.0 | 4.47 | 1290.0 | Gavrilov, 1980 |
| Tetrao urogallus (♀) | 3900 | W | 1376.3 | 4.11 | 1253.0 | Gavrilov, 1980 |
| <u>Gruiformes</u> | | | | | | |
| Crex crex | 140 | S | 276.6 | 5.18 | 121.2 | Gavrilov (in press) |
| Crex crex | 162 | W | 285.1 | 4.98 | 135.7 | Gavrilov (in press) |
| Fulica atra | 407 | S | 497.4 | 7.11 | 284.3 | Gavrilov (in press) |
| Fulica atra | 407 | W | 470.6 | 7.13 | 256.7 | Gavrilov (in press) |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|----------------------------------|------|---|--------|-------|--------|---------------------------------|
| <i>Porphyrio plliocephalus</i> | 1820 | S | 1101.6 | 15.73 | 629.8 | Gavrillov (in press) |
| <i>Anthropoides virgo</i> | 2500 | S | 1357.8 | 17.80 | 823.6 | Gavrillov (in press) |
| <i>Otis tarda</i> | 4420 | W | 1700.8 | 13.09 | 130.0 | Gavrillov (in press) |
| <i>Grus grus</i> | 4480 | W | 1550.4 | 10.69 | 1229.8 | Gavrillov (in press) |
| <i>Grus japonensis</i> | 8130 | W | 2203.6 | 13.48 | 1799.1 | Gavrillov (in press) |
| <u>Charadriiformes</u> | | | | | | |
| <i>Charadrius dubius</i> | 36.4 | S | 110.5 | 2.27 | 42.7 | Gavrillov, 1981 |
| <i>Charadrius hiaticula</i> | 52.4 | S | 139.0 | 2.25 | 71.6 | Gavrillov, 1981 |
| <i>Tringa hypoleucos</i> | 53.8 | S | 142.8 | 2.42 | 70.3 | Gavrillov, 1981 |
| <i>Tringa glareola</i> | 61.2 | S | 152.0 | 2.65 | 72.5 | Gavrillov, 1981 |
| <i>Phylomachus pygnae</i> | 167 | S | 260.9 | 3.94 | 142.8 | Gavrillov, 1981 |
| <i>Vanellus vanellus</i> | 220 | S | 302.7 | 4.45 | 169.2 | Gavrillov, 1981 |
| <i>Larus ridibundus</i> | 285 | S | 410.7 | 6.40 | 219.7 | Gavrillov, 1981 |
| <i>Larus ridibundus</i> | 285 | W | 386.9 | 6.32 | 197.2 | Gavrillov, 1981 |
| <i>Haematopus ostralegus</i> | 385 | W | 375.6 | 4.06 | 253.7 | Gavrillov, 1981 |
| <i>Larus canus</i> | 424 | S | 499.5 | 7.30 | 280.6 | Gavrillov, 1981 |
| <i>Scelopax rusticola</i> | 429 | W | 445.9 | 5.88 | 269.6 | Gavrillov, 1981 |
| <i>Cephus grylle</i> | 482 | W | 528.8 | 8.12 | 285.1 | Gavrillov, 1981 |
| <i>Numenius arquata</i> | 520 | W | 429.2 | 3.96 | 310.2 | Gavrillov, 1981 |
| <i>Uria lomvia</i> | 1320 | W | 668.2 | 4.22 | 541.8 | Gavrillov, 1981 |
| <i>Larus fuscus</i> | 1650 | S | 868.0 | 9.07 | 595.8 | Gavrillov, 1981 |
| <u>Columbiformes</u> | | | | | | |
| <i>Geopelia cuneata</i> | 29.6 | S | 118.1 | 2.62 | 39.3 | Gavrillov (unpublished) |
| <i>Geopelia cuneata</i> | 31.2 | W | 104.3 | 2.34 | 34.0 | Gavrillov (unpublished) |
| <i>Streptopelia senegalensis</i> | 108 | S | 221.1 | 3.94 | 103.0 | Gavrillov (unpublished) |
| <i>Streptopelia senegalensis</i> | 108 | W | 224.1 | 4.51 | 88.8 | Gavrillov (unpublished) |
| <i>Streptopelia turtur</i> | 162 | S | 258.3 | 4.30 | 129.3 | Gavrillov, Dolnik (unpublished) |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|--------------------------|-------|---|-------|-------|-------|--------------------------------|
| Columba livia | 353 | S | 408.7 | 5.78 | 235.3 | Gavrilov (unpublished) |
| Columba livia | 380 | W | 362.3 | 5.25 | 204.8 | Gavrilov (unpublished) |
| Columba palumbus | 593 | A | 501.6 | 6.00 | 321.6 | Gavrilov, Dolnik (unpublished) |
| <u>Psittaciformes</u> | | | | | | |
| Melopsittacus undulatus | 25.2 | S | 120.6 | 2.85 | 35.2 | Gavrilov (unpublished) |
| Melopsittacus undulatus | 28.4 | W | 111.2 | 2.70 | 30.1 | Gavrilov (unpublished) |
| Agapornis roseicollis | 48.1 | S | 184.6 | 4.31 | 55.3 | Gavrilov (unpublished) |
| Agapornis roseicollis | 48.1 | W | 170.2 | 4.07 | 48.1 | Gavrilov (unpublished) |
| Nymphicus hollandicus | 85.6 | S | 204.3 | 4.05 | 82.9 | Gavrilov (unpublished) |
| Nymphicus hollandicus | 108.4 | W | 187.4 | 3.38 | 86.0 | Gavrilov (unpublished) |
| Calyptorhynchus funereus | 670 | S | 645.6 | 10.73 | 323.7 | Gavrilov, Dolnik (unpublished) |
| Prolosciger atterimus | 680 | S | 636.8 | 10.12 | 333.2 | Gavrilov, Dolnik (unpublished) |
| <u>Cuculiformes</u> | | | | | | |
| Cuculus canorus | 106 | S | 246.6 | 5.14 | 92.5 | Gavrilov, Dolnik (unpublished) |
| Tauraco corithaix | 302 | S | 412.0 | 7.90 | 237.0 | Gavrilov, Dolnik (unpublished) |
| <u>Strigiformes</u> | | | | | | |
| Otus scops | 88 | S | 163.3 | 2.59 | 85.4 | Gavrilov (unpublished) |
| Otus scops | 92 | W | 148.5 | 2.44 | 75.3 | Gavrilov (unpublished) |
| Aegolius funereus | 138 | A | 243.3 | 3.95 | 124.8 | Gavrilov, Dolnik (unpublished) |
| Tuto alba | 246 | A | 345.0 | 5.86 | 169.1 | Gavrilov, Dolnik (unpublished) |
| Asio otus | 283 | S | 379.3 | 6.23 | 192.6 | Gavrilov, Dolnik (unpublished) |
| Stix aluco | 484 | W | 480.3 | 9.11 | 207.0 | Gavrilov, Dolnik (unpublished) |
| Nyctea scandiaca | 1970 | S | 802.6 | 23.82 | 87.9 | Gessaman, 1972 |
| <u>Coraciiformes</u> | | | | | | |
| Upupa epops | 49.9 | S | 150.7 | 3.06 | 59.0 | Gavrilov (unpublished) |
| Upupa epops | 52.8 | W | 141.8 | 2.93 | 54.0 | Gavrilov (unpublished) |
| Dacelo novaeguinea | 350 | S | 425.8 | 8.16 | 180.9 | Gavrilov, Dolnik (unpublished) |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|-------------------------|------|---|-------|------|-------|--------------------------------|
| <u>Piciformes</u> | | | | | | |
| Dendrocopus pubescens | 27.3 | W | 126.0 | 1.69 | 75.4 | Koplin, 1972 |
| Lynx torquilla | 31.8 | S | 113.9 | 2.46 | 40.1 | Gavrilov, Dolnik (unpublished) |
| Dendrocopus villosus | 63.1 | W | 202.2 | 2.57 | 125.2 | Koplin, 1972 |
| Dendrocopus major | 98.0 | S | 196.0 | 2.26 | 128.0 | Gavrilov (unpublished) |
| Dendrocopus major | 98.0 | W | 176.3 | 2.13 | 112.2 | Gavrilov (unpublished) |
| <u>Passeriformes</u> | | | | | | |
| Regulus regulus | 5.5 | A | 45.2 | 0.78 | 21.7 | Gavrilov, 1982 |
| Phylloscopus collybita | 6.5 | A | 51.9 | 0.95 | 23.4 | Gavrilov, 1982 |
| Phylloscopus sibilatrix | 7.6 | S | 57.8 | 1.14 | 23.5 | Gavrilov, 1982 |
| Estrilda troglodytes | 7.7 | S | 67.0 | 1.48 | 22.6 | Gavrilov, 1982 |
| Estrilda troglodytes | 7.7 | W | 64.2 | 1.33 | 24.3 | Gavrilov, 1982 |
| Tiaris canora | 7.8 | S | 67.4 | 1.44 | 24.3 | Gavrilov, 1982 |
| Aegithalos candatus | 8.8 | S | 62.0 | 1.22 | 25.4 | Gavrilov, 1982 |
| Aegithalos candatus | 8.8 | W | 60.7 | 1.09 | 28.1 | Gavrilov, 1982 |
| Troglodytes troglodytes | 9.0 | S | 62.4 | 1.18 | 26.8 | Gavrilov, 1982 |
| Troglodytes troglodytes | 9.0 | W | 58.6 | 0.96 | 29.7 | Gavrilov, 1982 |
| Uraeginthus bengalis | 9.2 | S | 7.4 | 1.35 | 26.8 | Gavrilov, 1982 |
| Uraeginthus bengalis | 9.2 | W | 62.5 | 1.24 | 25.3 | Gavrilov, 1982 |
| Sporophila nitricollis | 9.3 | S | 75.4 | 1.68 | 25.0 | Cox, 1961 |
| Sporophila nigricollis | 9.3 | W | 59.5 | 1.10 | 26.5 | Cox, 1961 |
| Volatina jacarina | 9.4 | S | 68.2 | 1.36 | 27.6 | Cox, 1961 |
| Volatina jacarina | 9.4 | W | 58.2 | 1.08 | 25.7 | Cox, 1961 |
| Parus ater | 9.7 | S | 65.3 | 1.23 | 28.4 | Gavrilov, 1982 |
| Parus ater | 9.7 | W | 62.0 | 1.05 | 30.6 | Gavrilov, 1982 |
| Phylloscopus trochilus | 9.8 | S | 68.2 | 1.59 | 20.5 | Gavrilov, 1982 |
| Phylloscopus trochilus | 9.8 | A | 66.1 | 1.23 | 29.4 | Gavrilov, 1982 |
| Lonchura striata | 10.3 | S | 71.6 | 1.37 | 30.5 | Gavrilov, 1982 |
| Lonchura striata | 10.3 | W | 72.4 | 1.59 | 24.6 | Gavrilov, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|----------------------------------|------|---|------|------|------|-------------------------|
| <i>Sylvia curruca</i> | 10.3 | S | 68.2 | 1.24 | 30.9 | Gavrillov, 1982 |
| <i>Sporophila aurita</i> | 10.7 | S | 75.4 | 1.42 | 32.7 | Cox, 1961 |
| <i>Sporophila aurita</i> | 10.7 | W | 67.0 | 1.18 | 31.6 | Cox, 1961 |
| <i>Parus palustris</i> | 11.1 | S | 67.8 | 1.17 | 32.7 | Gavrillov, 1982 |
| <i>Ficedula hypoleuca</i> | 11.2 | A | 70.3 | 1.30 | 31.3 | Gavrillov, 1982 |
| <i>Acrocephalus schoenobenus</i> | 11.5 | S | 72.8 | 1.34 | 32.7 | Gavrillov, 1982 |
| <i>Phoenicurus phoenicurus</i> | 11.6 | A | 69.1 | 1.18 | 33.5 | Gavrillov, 1982 |
| <i>Spinus spinus</i> | 12.0 | S | 68.7 | 1.10 | 35.8 | Gavrillov, 1982 |
| <i>Spinus spinus</i> | 12.0 | W | 66.6 | 0.99 | 36.8 | Gavrillov, 1982 |
| <i>Taeniopygia castanotis</i> | 12.1 | W | 75.4 | 1.59 | 27.6 | El-Wailly, 1966 |
| <i>Taeniopygia castanotis</i> | 12.3 | S | 70.8 | 1.52 | 25.3 | Gavrillov (unpublished) |
| <i>Taeniopygia castanotis</i> | 12.5 | W | 64.5 | 1.20 | 28.4 | Gavrillov (unpublished) |
| <i>Serinus canaria</i> | 12.8 | S | 70.6 | 1.34 | 30.5 | Gavrillov, 1982 |
| <i>Serinus canaria</i> | 12.2 | W | 70.3 | 1.05 | 38.9 | Gavrillov, 1982 |
| <i>Sylvia communis</i> | 13.1 | S | 78.4 | 1.38 | 37.0 | Gavrillov, 1982 |
| <i>Sylvia communis</i> | 13.1 | A | 73.3 | 1.17 | 38.1 | Gavrillov, 1982 |
| <i>Spizella pusilla</i> (♀) | 13.2 | S | 67.8 | 1.21 | 31.6 | Olson, 1965 |
| <i>Spizella pusilla</i> (♀) | 13.2 | W | 61.5 | 1.09 | 28.8 | Olson, 1965 |
| <i>Spizella pusilla</i> (♂) | 13.9 | S | 69.5 | 1.23 | 32.4 | Olson, 1965 |
| <i>Spizella pusilla</i> (♂) | 13.9 | W | 65.3 | 1.19 | 29.5 | Olson, 1965 |
| <i>Acanthis flammea</i> | 13.5 | S | 71.2 | 1.05 | 39.5 | Gavrillov, 1982 |
| <i>Acanthis flammea</i> | 13.5 | W | 67.4 | 1.00 | 37.3 | Gavrillov, 1982 |
| <i>Acanthis flammea</i> | 14.6 | S | 84.6 | 1.43 | 41.7 | Grooks, 1968 |
| <i>Acanthus flammea</i> | 14.6 | W | 65.3 | 0.90 | 38.3 | Brooks, 1968 |
| <i>Phoenicurus ochruros</i> | 14.0 | S | 77.9 | 1.37 | 36.8 | Gavrillov, 1982 |
| <i>Eriothacus rubecula</i> | 14.0 | S | 78.7 | 1.45 | 33.1 | Gavrillov, 1982 |
| <i>Eriothacus rubecula</i> | 14.0 | W | 76.2 | 1.34 | 36.0 | Gavrillov, 1982 |
| <i>Hippolais icterina</i> | 14.1 | S | 80.4 | 1.45 | 36.8 | Gavrillov, 1982 |
| <i>Acanthis cannabina</i> | 14.5 | S | 74.5 | 1.14 | 40.2 | Gavrillov, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---------------------------------|------|---|-------|------|------|----------------|
| <i>Acanthis cannabina</i> | 14.5 | A | 79.5 | 1.34 | 39.4 | Gavrilov, 1982 |
| <i>Acanthis hornemanni</i> | 14.5 | S | 82.1 | 1.36 | 41.4 | Brooks, 1968 |
| <i>Acanthis hornemanni</i> | 14.5 | W | 65.3 | 1.07 | 33.3 | Brooks, 1968 |
| <i>Motacilla flava</i> | 15.4 | S | 81.6 | 1.38 | 40.2 | Gavrilov, 1982 |
| <i>Saxicola rubetra</i> | 15.7 | S | 82.9 | 1.39 | 41.1 | Gavrilov, 1982 |
| <i>Carduelis carduelis</i> | 15.8 | S | 86.9 | 1.28 | 48.5 | Gavrilov, 1982 |
| <i>Carduelis carduelis</i> | 15.9 | W | 78.7 | 1.18 | 43.2 | Gavrilov, 1982 |
| <i>Prunella modularis</i> | 16.5 | A | 82.9 | 1.35 | 42.3 | Gavrilov, 1982 |
| <i>Parus major</i> | 17.0 | S | 85.4 | 1.34 | 45.1 | Gavrilov, 1982 |
| <i>Parus major</i> | 17.0 | W | 80.4 | 1.28 | 38.6 | Gavrilov, 1982 |
| <i>Anthus pratensis</i> | 17.5 | S | 89.6 | 1.59 | 41.9 | Gavrilov, 1982 |
| <i>Motacilla alba</i> | 18.0 | S | 87.1 | 1.43 | 44.1 | Gavrilov, 1982 |
| <i>Motacilla alba</i> | 18.0 | W | 82.1 | 1.36 | 41.4 | Gavrilov, 1982 |
| <i>Emberiza schoeniclus</i> | 18.2 | S | 87.9 | 1.30 | 49.0 | Gavrilov, 1982 |
| <i>Emberiza schoeniclus</i> | 18.2 | W | 87.1 | 1.39 | 45.3 | Gavrilov, 1982 |
| <i>Luscinia svecica</i> | 18.2 | A | 90.4 | 1.59 | 42.7 | Gavrilov, 1982 |
| <i>Spizella arborea</i> | 19.0 | S | 94.6 | 1.53 | 48.6 | West, 1960 |
| <i>Spizella arborea</i> | 19.0 | W | 77.9 | 1.03 | 46.8 | West, 1960 |
| <i>Junco hyemalis</i> | 19.4 | S | 89.6 | 1.08 | 57.1 | Seibert, 1949 |
| <i>Junco hyemalis</i> | 19.4 | W | 72.0 | 0.64 | 52.9 | Seibert, 1949 |
| <i>Sylvia atricapilla</i> | 20.0 | S | 97.1 | 1.75 | 44.8 | Gavrilov, 1982 |
| <i>Sylvia atricapilla</i> | 20.4 | A | 90.2 | 1.66 | 40.3 | Gavrilov, 1982 |
| <i>Fringilla coelebs</i> | 20.0 | S | 101.7 | 1.73 | 49.9 | Gavrilov, 1982 |
| <i>Fringilla coelebs</i> | 20.0 | W | 89.2 | 1.52 | 49.9 | Gavrilov, 1982 |
| <i>Fringilla coelebs</i> | 20.0 | S | 87.9 | 1.39 | 46.2 | Dolnik, 1974 |
| <i>Fringilla coelebs</i> | 20.0 | W | 85.8 | 2.24 | 18.6 | Dolnik, 1974 |
| <i>Sylvia nisoria</i> | 20.6 | S | 101.3 | 1.81 | 46.9 | Gavrilov, 1982 |
| <i>Fringilla montifringilla</i> | 21.0 | S | 90.2 | 1.19 | 54.4 | Gavrilov, 1982 |
| <i>Fringilla montifringilla</i> | 21.0 | W | 94.6 | 1.37 | 53.5 | Gavrilov, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|-----------------------|------|---|-------|------|------|----------------|
| Carpodacus erythrinus | 21.0 | S | 110.5 | 1.75 | 58.2 | Gavrilov, 1982 |
| Carpodacus erythrinus | 21.0 | W | 98.4 | 1.60 | 50.3 | Gavrilov, 1982 |
| Sylvia borin | 22.0 | S | 109.1 | 1.84 | 54.0 | Gavrilov, 1982 |
| Sylvia borin | 22.0 | A | 95.9 | 1.45 | 52.3 | Gavrilov, 1982 |
| Passer d. bactrianus | 22.2 | S | 110.1 | 1.77 | 57.0 | Gavrilov, 1982 |
| Passer d. bactrianus | 22.2 | W | 96.7 | 1.56 | 49.9 | Gavrilov, 1982 |
| Passer domesticus | 25.0 | S | 103.4 | 1.31 | 64.2 | Gavrilov, 1982 |
| Passer domesticus | 25.0 | W | 98.8 | 1.14 | 64.5 | Gavrilov, 1982 |
| Passer domesticus | 25.2 | S | 107.6 | 1.34 | 67.4 | Kendeigh, 1949 |
| | | | | | | Davis, 1955 |
| Passer domesticus | 25.2 | W | 103.4 | 1.14 | 69.2 | Kendeigh, 1949 |
| | | | | | | Davis, 1955 |
| Passer montanus | 22.5 | S | 99.0 | 1.49 | 54.2 | Gavrilov, 1982 |
| Passer montanus | 22.5 | W | 97.1 | 1.56 | 50.3 | Gavrilov, 1982 |
| Emberiza leucocephala | 22.5 | W | 95.5 | 1.56 | 48.6 | Gavrilov, 1982 |
| Anthus campestris | 23.1 | A | 101.3 | 1.59 | 53.6 | Gavrilov, 1982 |
| Anthus trivialis | 23.2 | A | 104.3 | 1.79 | 50.6 | Gavrilov, 1982 |
| Lullula arborea | 23.8 | S | 98.4 | 1.01 | 68.0 | Gavrilov, 1982 |
| Lullula arborea | 25.0 | W | 101.3 | 1.31 | 62.0 | Gavrilov, 1982 |
| Lanius collurio | 25.3 | S | 101.3 | 1.39 | 59.5 | Gavrilov, 1982 |
| Lanius collurio | 26.2 | A | 104.8 | 1.41 | 62.5 | Gavrilov, 1982 |
| Carduelis chloris | 26.5 | S | 108.0 | 1.37 | 66.9 | Gavrilov, 1982 |
| Carduelis chloris | 26.5 | W | 98.4 | 1.29 | 59.7 | Gavrilov, 1982 |
| Emberiza hortulana | 26.5 | S | 114.7 | 1.74 | 62.6 | Gavrilov, 1982 |
| Emberiza hortulana | 26.5 | W | 107.2 | 1.59 | 59.5 | Gavrilov, 1982 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|--------------------------------------|------|---|-------|------|-------|---------------------------------------|
| <i>Emberiza citrinella</i> | 27.1 | S | 112.6 | 1.73 | 60.7 | Gavrilov, 1982 |
| <i>Emberiza citrinella</i> | 27.1 | W | 101.7 | 1.30 | 62.7 | Gavrilov, 1982 |
| <i>Zonotrichia albicollis</i> | 27.4 | W | 96.3 | 1.59 | 48.6 | Kontogiannis, 1968 |
| <i>Pyrrhula pyrrhula</i> | 30.4 | S | 125.8 | 1.71 | 74.5 | Gavrilov, 1982 |
| <i>Pyrrhula pyrrhula</i> | 30.4 | W | 110.1 | 1.56 | 63.6 | Gavrilov, 1982 |
| <i>Spiza americana</i> (♀) | 29.6 | S | 122.3 | 2.28 | 53.8 | Zimmerman, 1965 |
| <i>Spiza americana</i> (♀) | 29.6 | W | 102.2 | 2.17 | 37.1 | Zimmerman, 1965 |
| <i>Spiza americana</i> (♂) | 31.6 | S | 119.3 | 2.16 | 54.4 | Zimmerman, 1965 |
| <i>Spiza americana</i> (♂) | 31.6 | W | 108.4 | 2.25 | 41.0 | Zimmerman, 1965 |
| <i>Montifringilla nivalis</i> | 30.7 | S | 109.3 | 1.48 | 64.9 | Gavrilov, 1982 |
| <i>Petronia petronia</i> | 32.8 | S | 115.6 | 1.69 | 64.9 | Gavrilov, 1982 |
| <i>Petronia petronia</i> | 33.2 | W | 104.3 | 1.60 | 56.2 | Gavrilov, 1982 |
| <i>Eremophila alpestris</i> | 36.6 | S | 123.5 | 1.79 | 69.9 | Gavrilov, 1982 |
| <i>Aremonops conirostris</i> | 37.0 | S | 127.3 | 2.32 | 57.6 | Cox, 1961 |
| <i>Aremonops conirostris</i> | 37.0 | W | 123.1 | 2.32 | 53.5 | Cox, 1961 |
| <i>Alanda arvensis</i> | 39.4 | S | 130.6 | 1.84 | 75.4 | Gavrilov, 1982 |
| <i>Loxia curvirostra</i> | 44.7 | S | 135.6 | 1.39 | 93.8 | Gavrilov, 1982 |
| <i>Loxia curvirostra</i> | 44.7 | W | 128.1 | 1.24 | 90.8 | Gavrilov, 1982 |
| <i>Coccothraustes coccothraustes</i> | 48.2 | S | 152.3 | 1.80 | 98.4 | Gavrilov, 1982 |
| <i>Coccothraustes coccothraustes</i> | 48.2 | W | 141.9 | 1.64 | 92.6 | Gavrilov, 1982 |
| <i>Emberiza calandra</i> | 48.8 | S | 144.4 | 2.04 | 83.3 | Gavrilov, 1982 |
| <i>Loxia pytiopsittacus</i> | 53.4 | W | 138.2 | 1.16 | 103.4 | Gavrilov, 1982 |
| <i>Coccothraustes vespertinus</i> | 54.5 | W | 155.8 | 2.56 | 78.9 | West, Hart, 1966 |
| <i>Coccothraustes vespertinus</i> | 57.0 | S | 169.6 | 2.26 | 101.7 | I.E. Williams (Kendeigh et al., 1977) |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|-------------------------|------|---|-------|------|-------|----------------|
| Turdus iliacus | 54.0 | A | 157.0 | 2.09 | 94.2 | Gavrilov, 1979 |
| Oriolus oriolus | 65.1 | S | 169.1 | 2.22 | 102.6 | Gavrilov, 1982 |
| Lanius exubitor | 71.3 | A | 177.1 | 2.27 | 108.9 | Gavrilov, 1982 |
| Sturnus valgeris | 78.0 | S | 201.4 | 2.57 | 124.3 | Gavrilov, 1982 |
| Sturnus vulgaris | 78.0 | W | 179.2 | 2.05 | 117.6 | Gavrilov, 1982 |
| Turdus philomelos | 80.0 | S | 218.1 | 2.92 | 130.6 | Gavrilov, 1979 |
| Turdus philomelos | 80.0 | W | 187.2 | 2.55 | 110.5 | Gavrilov, 1979 |
| Turdus marula | 83.0 | S | 193.9 | 1.93 | 135.8 | Gavrilov, 1979 |
| Turdus merula | 83.0 | W | 180.9 | 1.91 | 123.5 | Gavrilov, 1979 |
| Cyanocitta cristata | 84.5 | S | 244.1 | 2.03 | 183.2 | Clemans, 1974 |
| Cyanocitta cristata | 84.5 | W | 240.3 | 3.47 | 136.2 | Clemans, 1974 |
| Turdus visciivorus | 112 | A | 223.6 | 2.52 | 147.8 | Gavrilov, 1979 |
| Nucifraga caryocatactes | 147 | W | 247.0 | 2.26 | 179.2 | Gavrilov, 1979 |
| Garrulus glandarius | 153 | W | 255.4 | 2.75 | 173.0 | Gavrilov, 1979 |
| Pica pica | 205 | W | 297.7 | 2.60 | 219.8 | Gavrilov, 1979 |
| Pyrrhocorax graculus | 208 | W | 298.1 | 2.73 | 216.1 | Gavrilov, 1979 |
| Coleus monedula | 215 | W | 305.6 | 3.04 | 214.3 | Gavrilov, 1979 |
| Corvus frugilegus | 390 | W | 410.3 | 2.18 | 345.0 | Gavrilov, 1979 |
| Corvus corone cornix | 540 | S | 494.5 | 2.98 | 405.0 | Gavrilov, 1979 |
| Corvus corone cornix | 540 | W | 483.6 | 2.94 | 395.3 | Gavrilov, 1979 |
| Corvus ruficollis | 660 | W | 532.2 | 1.41 | 484.8 | Gavrilov, 1979 |
| Corvus corax | 1203 | S | 814.8 | 3.06 | 723.0 | Gavrilov, 1979 |
| Corvus corax | 1203 | W | 783.8 | 2.65 | 704.3 | Gavrilov, 1979 |

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Symposium

PHOTOPERIODIC CONTROL AND ENDOGENOUS TIME PROGRAMS

Convener: B. FOLLETT, UK

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CHANDOLA A., SINGH S., CHAKRAVORTY K.

REPRODUCTIVE PERIODICITY IN THE WEAVER BIRD: ROLE OF PHOTOPERIOD
AND GONADAL HORMONES

WINGFIELD J.C.

ENVIRONMENTAL FACTORS INFLUENCING THE TERMINATION OF REPRODUCTI-
ON IN FINCHES

GAVRILOV V.M., DOBRYNINA I.N.

THE PHOTOPERIODIC CONTROL OF AN ENDOGENOUS TIMER REGULATING
POSTNUPTIAL MOULT IN BIRDS

GWINNER E., DITTAMI J., GÄNSHIRT G., HALL M., WOZNIAK J.

EXOGENOUS AND ENDOGENOUS COMPONENTS IN THE CONTROL OF THE
ANNUAL REPRODUCTIVE CYCLE OF THE EUROPEAN STARLING

WADA M.

GONADOTROPIN RELEASE AND RHYTHMS OF CALLING BEHAVIOUR BY
ENDOGENOUS OSCILLATOR IN QUAIL

REPRODUCTIVE PERIODICITY IN THE WEAVER BIRD:

ROLE OF PHOTOPERIOD AND OF GONADAL HORMONES

Asha Chandola, Sushama Singh, Krishna Chakravorty

Department of Zoology, Garhwal University, Srinagar, Garhwal, UP;

Department of Zoology, Banaras Hindu University, Varanasi, India

INTRODUCTION

Seasonality in reproduction is well marked in animals from the tropics and subtropics despite the somewhat less pronounced seasons. Whilst a number of environmental factors may be involved, from our recent studies on two bird models, viz., the Weaver Bird (Ploceus philippinus) and Spotted Munia (Lonchura Punctulata), it is fairly clear that variations in day length, despite minor annual fluctuations, might serve as a cue to time seasonal reproduction at these latitudes. Sharing similar distribution in the Indian Subcontinent, these two birds seem to use the photoperiod in different ways. In one (Weaver) as a "driving agent" directly providing the stimulus in the other (Spotted Munia) as a "synchroniser" serving to synchronise an endogenous circannual rhythm of reproduction with the most propitious time of the year (see reviews Chandola et al, 1982 a,b). Whichever way the information may be used the ultimate aim is reproductive preparation ensuring birth of the young ones when conditions for their upbringing are most favourable. For the successful survival of a species, however, the appropriate timing of the cessation of reproductive activity is as important as the offspring being born at the most propitious time. A look at the literature would reveal that while voluminous information exists on the control of onset of seasonal reproduction, relatively little is known about the termination of breeding. We now address ourselves to the regulation of seasonal reproduction in the subtropical Weaver bird, with an emphasis on the factors involved in the termination of reproductive activity.

REPRODUCTIVE CYCLE AND ENVIRONMENTAL FACTORS

The Weaver finch (Ploceus philippinus) is a seasonally breeding sedentary species distributed all over the Indian subcontinent. The present review is based upon studies carried out on locally caught bird populations at Varanasi (longitude 83° 01'E; latitude 25° 18'N). The seasonal changes in the environment at this latitude reflect the predominantly monsoon climate of the Subcontinent. Differences in the seasons are marked, apart from the temperature, by rainfall too. After winter solstice (10h 26 min. day length, 15°C average) with increasing day length, the temperature rises reaching maximum in late May (average 32°C). Early summer is thus characterised by scorching hot days, a dried out landscape and a scarcity of food. Monsoon showers in late summer are an abrupt relief and drastically change the environment. The clouds overcast the sky for days, altogether thus decreasing the light intensity and probably even cut short the day length. Heavy monsoon showers clear the sky from dust particles, thus allowing greater ultra-violet radiation on the earth. There is an immediate increase in vegetation and in insect population. The major grain crop "Kharif" also becomes available by the end of monsoon.

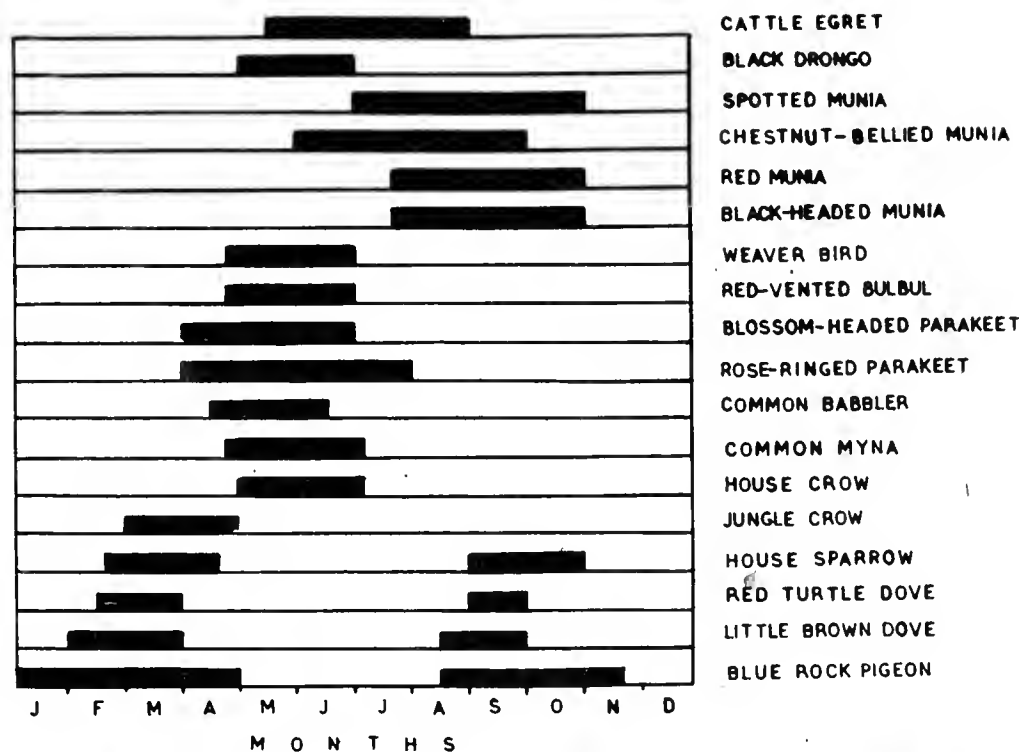


Fig. 1. Gonadal cycles of some of the Indian birds studied at Varanasi (25°18'N, 83°01'E)

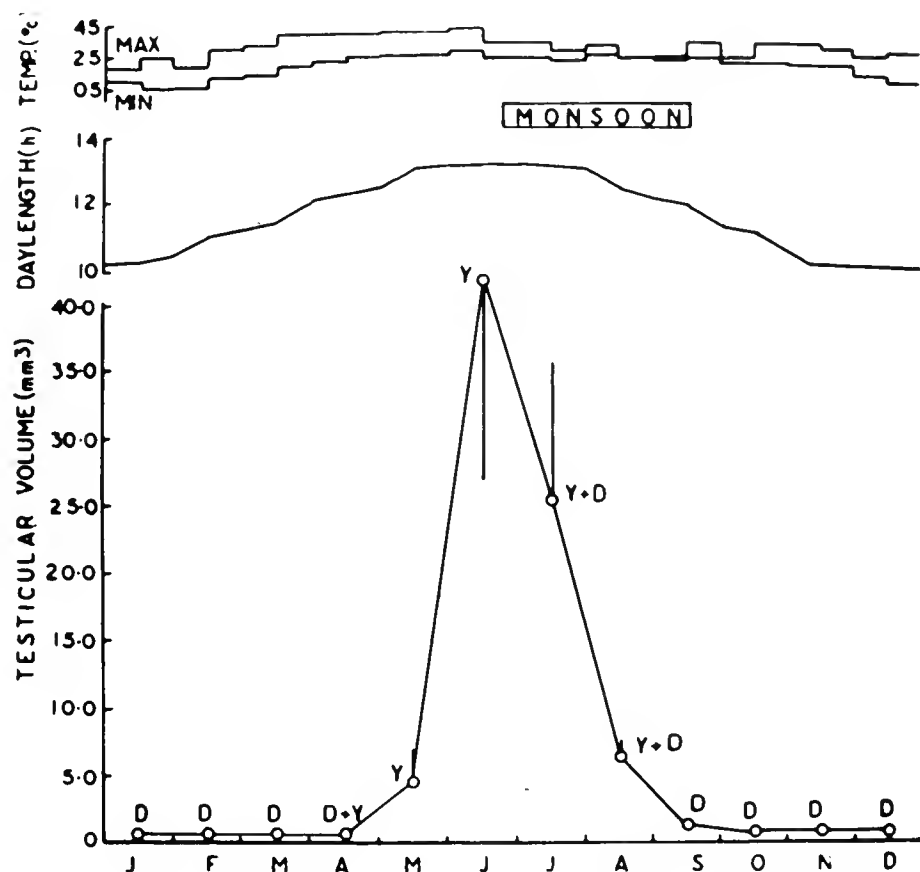


Fig. 2. Reproductive cycle of male Weaver Bird at Varanasi. Y - yellow plumage, D - dull plumage; the vertical lines indicate S.E.

Figure 1 lists the gonadal cycles of a number of birds studied at Varanasi (for references see Chandola et al., 1982b). The semi-domestic/domestic type shows an increased reproductive potential which is understandable, bearing in mind their more or less constant assurance of food supply. Among the wild forms, reproductive climax in some coincides with the first monsoon showers, whilst the others enter reproduction with the onset of monsoon. The Weaver Bird belongs to the first category. The male birds do on a characteristic yellow plumage after the prenuptial moulting in April, when gonadal development is initiated (Fig. 2). With an increase in gonadal volume primary and secondary spermatocytes appear in the seminiferous tubules in the month of April. Intertubular lumen formation occurs in early May and first spermatozoa appear in the latter half. The peak of gonadal activity in both the male and female is reached in June. In July gonads rapidly regress reaching the quiescent state by September, when nuptial plumage is shed off in males.

The yellow plumage in the Weaver, as in many finches (Witschi, 1955; Thapliyal, Tewary, 1964), is Luteinising hormone (LH) dependent (Thapliyal, Saxena, 1961). This appearance of pigmented yellow plumage indicates activation of pituitary gonadotrophic activity, as is also now clear from the estimation of plasma LH (Saxena et al., 1982, our unpublished results in collaboration with B.K.Follett). Beak pigmentation in this bird reflects gonadal activity. Castration causes a bleaching and testosterone administration to blackening of the beak.

Observations on annual variations in environmental factors in relation to the reproductive cycle indicate that the onset of gonadal activity in the Weaver Bird follows the increase in day length. Arrival of the monsoon coincides with the termination of gametogenetic activity, and commencement of oviposition. The hatching period coincides with a sudden increase in trophic resources, mainly insects during monsoon period.

ONSET OF BREEDING: THE PHOTOPERIODIC STIMULES

It is clear that gonadal development in the Weaver Bird begins much earlier than the arrival of the monsoon at Varanasi. For a precise timing of the breeding phase, it is imperative that the most propitious season be predicted well in advance of the reproductive climax i.e. nest building and egg laying, thus allowing sufficient time for the growth of the gonads (Farner, 1975). Considerable experimental information is available indicating that the increasing day length of spring might serve as a cue for the onset of breeding in the Weaver Bird (Thapliyal, Saxena, 1964; Thapliyal, Garg, 1968; Chandola et al., 1973, 1974, 1982a; Chandola, Thapliyal, 1976, 1978; Singh, Chandola, 1981a, 1982a).

Initiation of gonadal development occurs in 11-12 h artificial daily photoperiod (spring day length) and maximal gonadal activity is obtained in 13 h (summer day length) or longer daily photoperiod (Fig. 3). The reproductive cycle (as judged by yellow plumage, gonadal volume/histology) is completely suppressed in short day length, and extended long days maintain the gonads indefinitely active (Fig. 4). These findings suggest that adequate day length is a prerequisite for gonadal growth in this bird and appears to be acting as a driving agent. It has been clearly demonstrated that during onset of breeding, photoperiod directly stimulates the hypothalamo-hypophyseal system and not through effects on hypothalamo/hypophyseal sensitivity to gonadal feed-back (Singh, Chandola, 1981b). Photoreception, as in other birds, is extra-retinal (Singh, Pavgi, 1979). Endogenous circadian rhythms of photosensitivity have also been demonstrated in asymmetrical skeleton photoperiods, as well as resonance experiments (Singh nee Pavgi, 1979). Increasing day length of spring perhaps lead to gonadal development as a result of an interaction with circadian components (see Farner, 1975; Farner, Lewis, 1971; Farner, Follett, 1980; Follett, 1973).

TERMINATION OF BREEDING

Decline in Photosensitivity

Gonads of the Weaver Bird after reaching the peak of activity by summer solstice regress rapidly in July and by September attain a state of complete

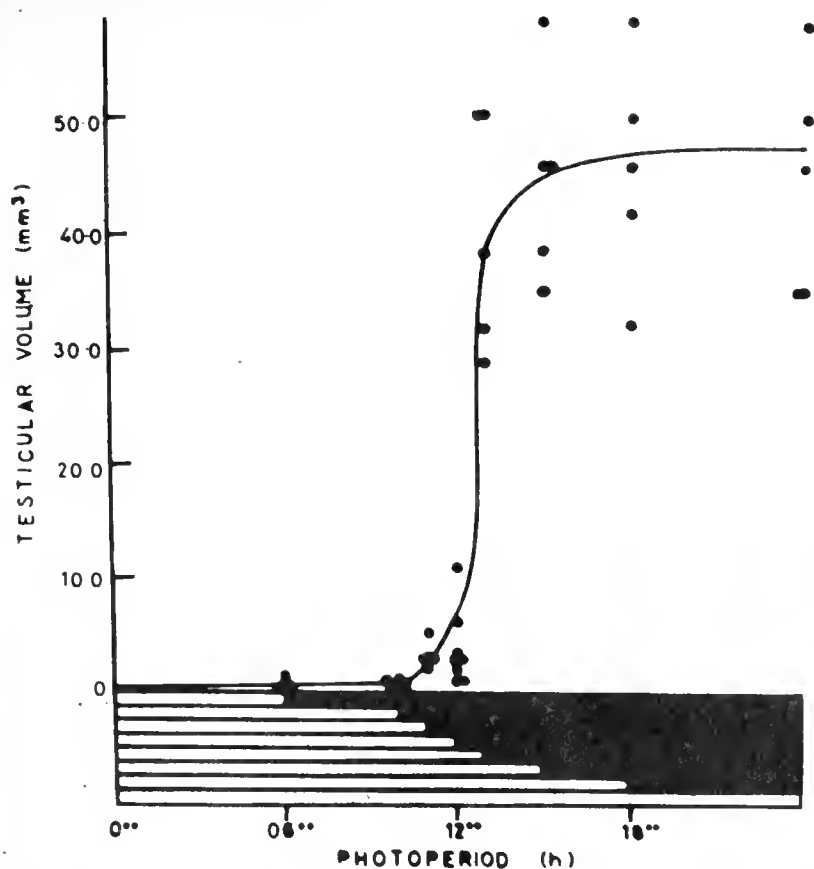


Fig. 3. Effects of various light/dark (L/D) schedules on the gonadal function of adult male Weaver Bird (45 days' treatment in spring)

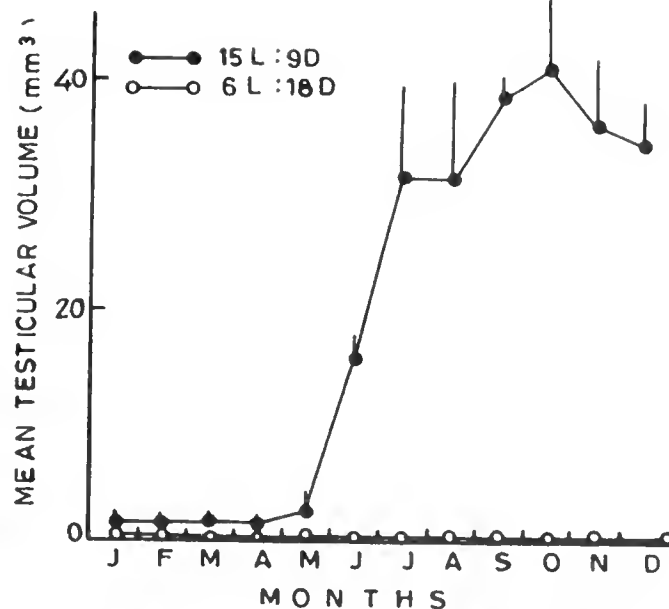


Fig. 4. Effects of constant long (15L/9D) and short (6L/18D) days on the testicular cycle of Weaver Bird

quiescence. The bird, therefore, becomes refractory in the sense that gonadal regression occurs despite the long days of summer. This is a typical situation encountered in photoperiodic species and has been referred to as "photorefractoriness". We have examined this process in detail in the Weaver Bird over the last few years which permits us some speculation. Not meaning to oversimplify, in as much as a response (or rather failure of response) to long days is concerned it appears to be a matter of degree of loss of photosensitivity. Termination in most temperate wild passerine forms is due to the development of an absolute photorefractoriness (total loss of photosensitivity) which has been described as spontaneous collapse and absence of redevelopment in continued long day length. It may be artificially induced by long days and in some cases may even be broken by long response to short days (Wolfson, 1952; Lofts, Murton, 1968; Farner, 1970, 1982; Dolnik, 1976; Farner, Follett, 1966, 1980).

In other forms loss of photosensitivity may not be complete eg. Weaver Bird. Continued exposure to long day length during regressed/regressing phase ultimately leads to gonadal recrudescence (Singh, Chandola, 1982a). Somewhat similar responses are obtained with Quails and Mallards which, however, may not represent the phenomenon in the wild (see discussion in Farner Follett, 1980). In a long term experiment (Singh, Chandola, 1981 b) birds were transferred from natural day length to continuous illumination (24L/0D) every month and observations for five successive months were made on body weight, testis size (*in situ* by laparotomy) beak pigmentation and appearance of yellow colour in the regenerating feathers on left breast (which after every observation were plucked and stored). Results indicate a seasonal variation in the photogonadal response (Fig. 5). Response during progressive phase is

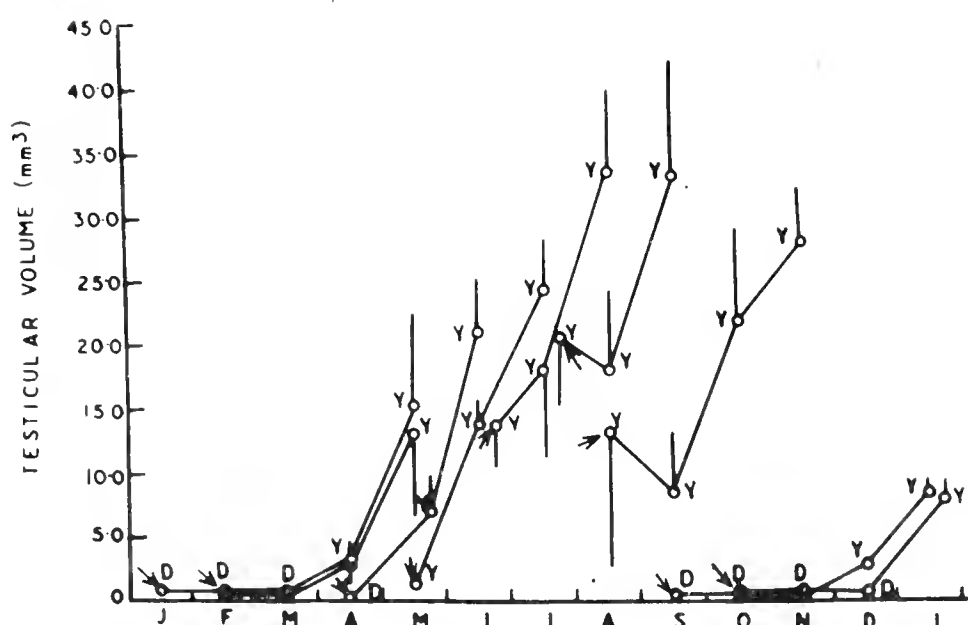


Fig. 5. Seasonal variation in the photogonadal response of the Weaver Bird. Arrows indicate transfer from natural day length to continuous illumination; other symbols as in Fig. 2

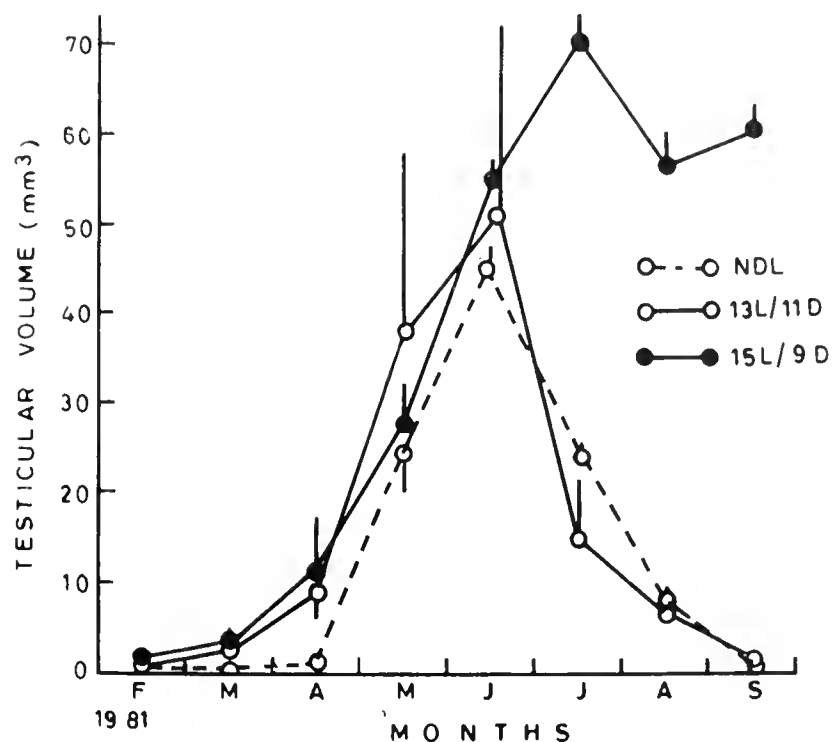
immediate but during sexual quiescence two to three months of exposure is required. Although birds never become totally insensitive to light, there is a progressive decline in photosensitivity coincident with gonadal regression. In April and May (early breeding) birds transferred to 24L/OD continued gonadal development reaching maximum. In June (late breeding) birds maintained high reproductive activity. During post-breeding regressive period (July/August) when gonads had begun to regress, but had not yet attained quiescence 24L/OD maintained the gonads for sometime, not allowing them to regress, followed by re-stimulation to peak level. Thus after the reproductive period gonads are still capable of responding to long days. This indicates gonadal regression is not the result of the development of a photorefractoriness, nevertheless the fact remains that in nature birds become refractory in the sense that although long day (which in artificial conditions affect maximal gonadal development) of June/July are available gonads regress. Birds are capable of responding to long day, long days are available yet gonads register a decline. It was suggested (Singh nee Pavgi, 1979; Singh, Chandola, 1981b) that an alteration in the photoperiodic response threshold had occurred which may have been set up at a higher level. Were this true gonads in stimulatory day lengths similar to that encountered in nature (at 25°N) would, after an initial stimulation, register decline-unlike in the very long days in which gonadal regression is eliminated. In a subsequent experiment (Chandola, Chakravorty, 1982) (Fig. 6), it was indeed found that while breeding in 15L/9D continued, gonads in 13L/9D regressed indicating that the day length which was stimulatory in spring is no more sufficient to permit gonadal activity. This would also explain cyclicity in 12L/12D (Singh, Chandola, 1981a) and prolonged gonadal activity in 15L/9D or 24L/OD.

It seems that the difference between the spring photoperiodic response threshold and the longest day length not being very great at 25°N, just a decline in the photosensitivity could terminate reproduction. In temperate zone birds the summer day lengths being very long, a mere decline may not serve the purpose hence the total insensitivity to photoperiod.

ROLE OF GONADAL HORMONES

Extensive castration studies have shown that sex hormones are implicated in termination of breeding in the Weaver Bird. The yellow plumage, shown to

Fig. 6. Comparative effects of two long day schedules (15L/9D and 13L/11D) on the gonadal cycle of male Weaver Bird. Note that 13L/9D which was stimulatory in Spring is not long enough in late summer to abolish regression



be LH dependent served as a good indicator of increased gonadotrophic secretion in circulation and hence of pituitary activity.

Castrates grow nuptial plumage which persists when intact birds are undergoing the normal plumage cycle. Although the elevated plasma LH levels may fall eventually the involvement of a steroidal feed-back in the seasonal inhibition of hypothalamo/hypophyseal gonadal system is clearly indicated. When birds were castrated every month over a period of one year (Fig. 7) it was evident that the response of hypothalamo/hypophyseal system to negative feed-back effect of testicular hormone changes with the phase of the reproductive cycle. Clearly the time of castration is critical. Similar findings have been made by Turek et al. (1981). In fact the feed-back in the Weaver is effective for a very limited period - two to three months just prior to regression, when the system is extremely sensitive in that even the non-stimulatory effects of artificial short days (6L/18D) (Fig. 8) are overridden (Singh, Chandola, 1981b). Thus birds castrated in the progressive period, regenerated yellow plumage, whereas those castrated during regressing and regressed phases, regenerated dull henny plumage (until the next breeding season). Clearly while sex steroids appear to inhibit the pituitary resulting in regression the quiescence of post reproductive period is not maintained because of sustained feed-back. Castration effects have been studied in a number of birds with reference to onset of photorefractoriness (Stetson, Erickson, 1971; Wilson, Follett, 1974; Hinde et al., 1974; Mattocks et al., 1976; Nicholls, Storey, 1976; Sharp, Moss, 1977; Stokkan, Sharp, 1980; Wingfield et al., 1980). In the Canary (Nicholls, Storey, 1976) plasma LH levels remain low after castration in photorefractory birds but in photorefractory Red Grouse plasma levels increase (Stokkan, Sharp, 1980). In the Weaver Bird both these effects (as judged by yellow plumage) were demonstrated in the same month (June) in birds in breeding conditions. The following experiment shows that while interpreting results, consideration must be given to the fact that although apparently similar in all reproductive aspects (hypothalamo/hypophyseal/gonadal activity), subtle changes might have occurred in the physiological status of the animal (not detectable otherwise) thus varying the response. Castration during fully breeding conditions (June) yielded two kinds of

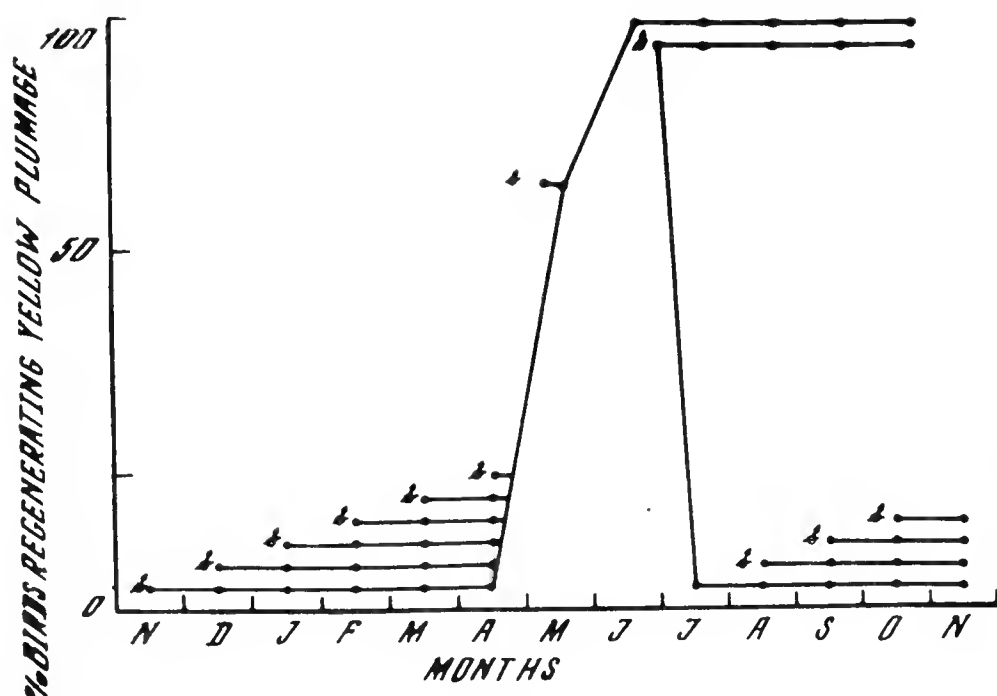


Fig. 7. Effect of castration on plumage of the male Weaver Bird during different months. Feathers on the left breast were plucked and the colour of the regenerating feathers noted

responses in the Weaver (Fig. 7). One half of birds regenerated yellow plumage whilst the rest developed dull henney plumage. When subsequently records on the extirpated gonads of this intriguing lot were checked, it was found that birds growing dull henney plumage had fully developed testis at the time of castration and those growing yellow plumage had testis large (and active) enough but not yet maximally grown. Obviously a change in the physiological status of the bird had occurred not allowing the effects of castration to be manifested at the hypothalamo/hypophyseal level.

This change does not involve an exhaustion of the pituitary (Miller, 1954; Nicolls, Storey, 1976) because it can be restimulated by photoperiod. Nor is it associated with the amount of light available since it was the same for both the groups. The photoperiodic stimulus is thus constant. In one group steroidal feed-back is operative, in other, not. If counteraction of the photo-stimulated hypothalamo/hypophyseal system by steroidal feed-back is merely a matter of appropriate hormonal thresholds being required to suppress the pituitary (see discussion in Urbanski, Follet, 1982) identical response should have been obtained for it is inconceivable that testicular hormone levels would be very different in an animal with near maximal testis from that with maximally grown testis. Obviously either the hypothalamo/hypophyseal system has been rendered insensitive to steroidal feed-back or some other intermediate hormones (thyroid, pineal, prolactin?) influenced by testicular secretions have intervened which are not allowing the feed-back to be expressed. In the Weaver Bird all three, thyroid (Thapliyal, Garg, 1968; Thapliyal, Bageshwar, 1970; Chandola et al., 1974), pineal hormones (Subramaniam, Saxena, 1974; Saxena, 1976) and prolactin (Thapliyal, Saxena, 1976) have been shown to be significantly antigonadal/antigonadotrophic.

STEROIDS VERSUS PHOTOPERIOD

It is evident from the preceding discussion that the reproductive cycle of the Weaver Bird is influenced remarkably by both - photoperiodic stimulation and steroidal feed-back. It is also clear that the response of the bird to both these influences varies seasonally. How far could these variations in responses be explained on the basis of an interaction of one with the other, and how do they actually modulate the seasonal cycle?

Reassessing the effects of castration in this light it is interesting that

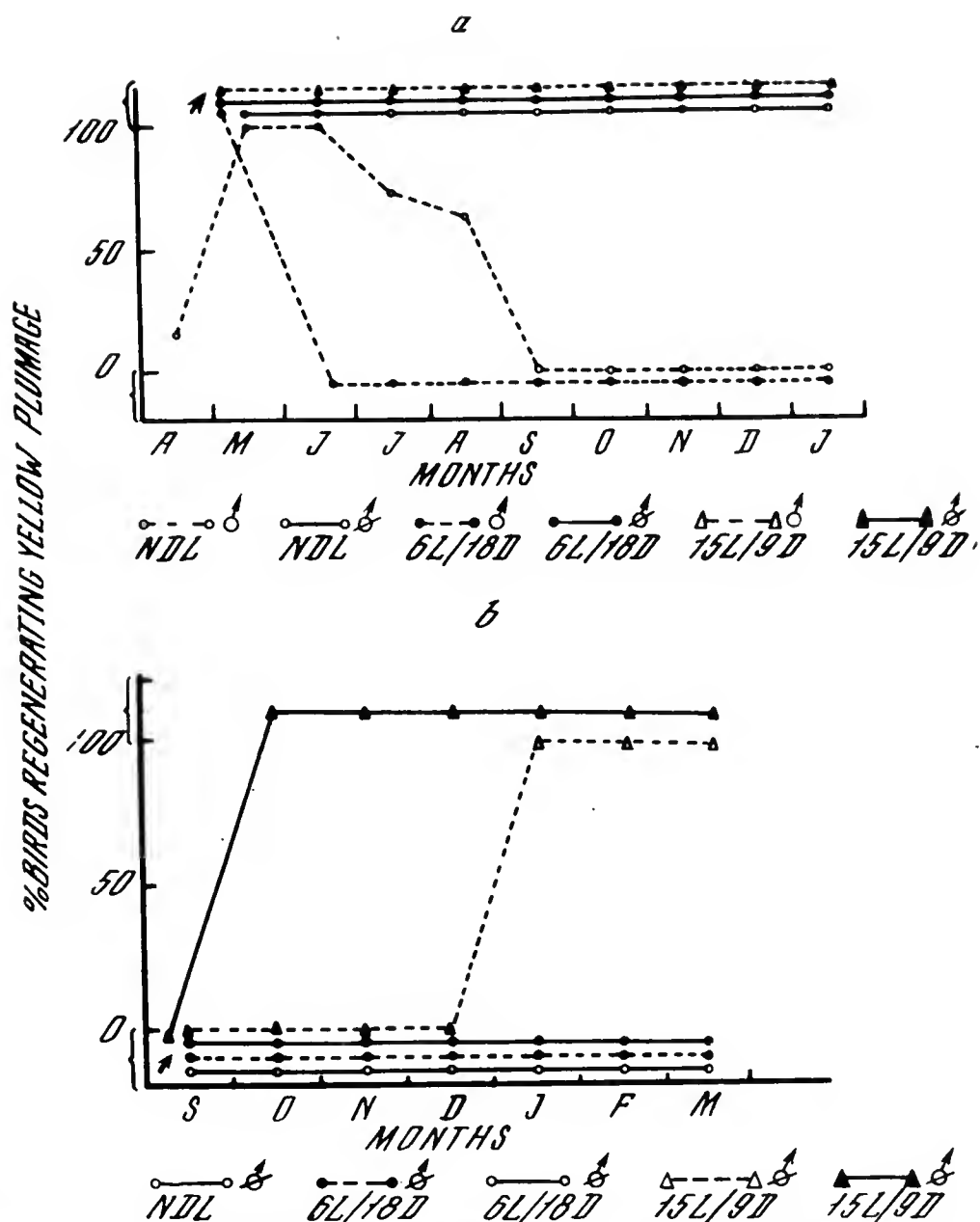


Fig. 8. Interaction of the effects of castration and photoperiod in the Weaver Bird; a - spring, b - autumn; arrows indicate commencement of treatment

irrespective of the month of castration yellow plumage made its appearance only in April/May and not before. In view of the photostimulatory effects of long days in this bird and the fact that in intact birds LH-dependent yellow plumage makes its appearance in April, when day length is increasing it can be concluded that the natural long days are responsible for the activation of the pituitary of the castrates. Long days therefore seem to directly stimulate the hypothalamo/hypophyseal system without affecting the sensitivity of the system to steroids. Similar observations have been made in Quail, Red Grouse, Tree Sparrow and Willow Ptarmigan (Gibson et al., 1975; Sharp, Moss, 1977; Wilson, Follett, 1974; Stokkan, Sharp, 1980a,b).

In July/August, however, castration did not lead to stimulation of pituitary activity despite the long day length of summer. In an experiment performed almost at the same time (Fig. 8) intact birds exposed to long photoperiod (15L/9D) required longer time for photostimulation but castrates exhibited yellow plumage through the very first regeneration. Clearly gonadal steroids alter the photoresponse during this period. But then if castration abolishes the delay in photoresponse the July/August castrates (Fig. 6) should respond to the available natural day length (13 h) which is certainly higher than the photoperiodic response threshold. It was suggested that the steroid feedback that had occurred at a higher day length of June might have lowered the photosensitivity of the bird by setting the threshold for photo-

periodic response at a higher level. Decreasing photoperiod thus would be insufficient to stimulate the hypothalamo/hypophyseal complex having a higher photoperiodic requirement than the available photoperiod. However, these speculations need to be further tested.

Comparing the seasonal effects of castration and photoperiod (Fig. 5, 7) decline in photosensitivity and loss of feed-back effect are observed at the same time at the onset of regression. Decline in photosensitivity is gradual, but loss of feed-back effect is abrupt. It is not known whether they are reflections of a single phenomenon or whether result from two distinct processes.

From our data it would seem:

a) enhanced circulating sex hormones of breeding apart from precipitating regression render the neuroendocrine system less sensitive to the effects of photoperiod;

b) sex hormones also stimulate secretion of hormones from thyroid, pineal and pituitary (prolactin) which keep the hypothalamo/hypophyseal system inhibited (thus interfering with gonadal photoresponse, as well as not permitting steroidal feed-back to be operative during that time.

The Weaver Bird having been reverentially approached every month, has revealed a number of possibilities amenable to exploration. It is evident that this bird shall prove an ideal tool in answering some basic questions in the physiology of seasonal reproduction.

SUMMARY

In the Weaver Bird (25°N) photoperiod appears to time the reproductive climax with the advent of monsoon when young ones are born. Long days (a prerequisite for gonadal growth in laboratory conditions) in spring cause gonadal development by a direct stimulation of the hypothalamo/hypophyseal system. Due to a decline in photosensitivity the long summer days are no more able to meet the photoperiodic requirement thus allowing steroid feed-back to precipitate regression. The decline in photosensitivity itself may be a result of steroidal interference at the level of higher photoresponding mechanisms. Although steroids may cause regression the sexual quiescence is not maintained because of a sustained steroidal feed-back. Thyroid and/or pineal hormones and/or prolactin (all anti-gonadal in the Weaver Bird) may keep the gonads inhibited during this period. In the Weaver Bird which is very photosensitive and inhabits the greatly insolated tropics, their role may assume great importance in modulating cyclicity.

ACKNOWLEDGEMENTS

The senior author thanks the University Grants Commission (India) for a Career Award and The Royal Society for a bursary in the U.K., where this manuscript was written. She also thanks Professor R.P.Ekins, Institute of Nuclear Medicine, Middlesex Hospital Medical School (London) for providing secretarial help and Mrs. Pat Landergan of the same Department for her able assistance in the preparation of this manuscript. Access to the reprint collection of Professor B.K.Follett, University of Bristol and financial assistance from the Indian National Science Academy and Department of Atomic Energy (India) is gratefully acknowledged.

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ENVIRONMENTAL FACTORS INFLUENCING THE TERMINATION OF REPRODUCTION IN FINCHES

John C. Wingfield

The Rockefeller University Field Research Centre, Tyrrel Road,
Millbrook, New York 12545, USA

INTRODUCTION

Reproduction in all avian species investigated to date is timed to coincide with periods of favorable trophic resources for feeding young (Lack, 1968; Perrins, 1970). In virtually all habitats, availability of food varies from season to season and year to year, and thus mechanisms have evolved whereby gonadal development is initiated several to many weeks in advance of amelioration of the environment so that the final reproductive effort, or nesting phase, can begin as soon as conditions permit (e.g. Marshall, 1960; Lofts, Murton, 1968; Immelmann, 1971, 1973; Murton, Westwood, 1977; Farner, Follett, 1979; Wingfield, 1980, 1982; Wingfield, Farner, 1980).

Equally important, however, are control systems that terminate the nesting phase before trophic resources decline. In many species that breed during the brief summers of high latitudes and altitudes, the nesting phase must also be terminated in sufficient time for post-nuptial moult and preparations for autumnal migration to be completed (Marshall, 1960; Lofts, Murton, 1968; Farner, Lewis, 1971; Dolnik, 1976; Murton, Westwood, 1977; Farner, Follett, 1979; Wingfield, Farner, 1980). On the other hand, reproduction in avian species that breed during the longer summers of mid-latitudes is often terminated in July and August, sometimes earlier. In these species the post-nuptial moult and preparations for migration are completed long before the first storms in October and November. Such an apparent "premature" termination of the nesting phase may be linked to availability of food for survival of young. For example, the Great Tit, Parus major, feeds its young primarily on caterpillars that are available for only a limited time in spring (Perrins, 1970, 1973). The energetic requirements for moult and when applicable, pre-migratory fat deposition, are satisfied by other foods that may not be suitable for the production and survival of young. Thus, in many species, mechanisms that terminate reproduction have reached a complex state of development owing to the need for precise timing in environments that undergo profound and predictable seasonal changes. These mechanisms include a refractory state in which individuals are no longer able to respond to environmental stimuli that initiated reproduction earlier in spring.

Refractory periods are by no means universal in avian breeding systems. A high level of endogenous nutrient reserves, especially protein, is apparently a major proximate factor timing the breeding seasons of several tropical avian species of southeast Asia and Indonesia (Fogden, 1972), the Yellow-vented Bulbul, Pycnonotus goiavier, (Ward, 1969), and the Grey-backed Camaroptera, Camaroptera brevicaudata, (Fogden, Fogden, 1979), and breeding terminates when these reserves become depleted. Whether this represents a refractory period, or just withdrawal of appropriate stimuli for breeding is open to question. In other tropical species perhaps as many as 10-20% exhibit some degree of overlap of reproduction and moult (Snow, 1962;

Stresemann, Stresemann, 1966; Immelmann, 1967; Foster, 1967; Wingfield, Farner, 1980). This coincidence of otherwise mutually exclusive events may be a reflection of the less precise and less predictable fluctuations of environmental conditions in some tropical habitats. In many species there may be no true refractory state since the non-breeding period, including the moult, can be interrupted and breeding commence immediately if conditions permit (Foster, 1975). In addition, opportunistic breeders of arid regions maintain the gonads at a near functional level so that breeding can begin as soon as conditions allow, e.g. the Zebra Finch, Poephila guttata, (Sossinka, 1974; Farner, Follett, 1979). A few species of northern latitudes may also lack a true refractory period. The gonads of the Red Crossbill, Loxia curvirostra, show a limited response to increasing day length, but breeding can occur at any time of year depending upon unpredictable crops of their principle food, the cones of coniferous trees (Tordoff, Dawson, 1965). Payne (1969) was able to stimulate gonadal growth in Tri-coloured Blackbirds, Agelaius tricolor, in autumn by providing insect food rich in protein. Similarly in Pinyon Jays, Gymnorhinus cyanocephalus, autumnal gonadal regression can be reversed by exposure to cones of the Pinyon Pine, Pinus edulis, a major item in the diet (Ligon, 1974).

PROTOPERIODIC CONTROL OF REFRACTORY PERIODS

In temperate and northern regions, it is well established that the vernal increase in day length initiates gonadal growth in anticipation of the ensuing breeding season (e.g., Marshall, 1960; Lofts, Murton, 1968; Farner, Lewis, 1971; Murton, Westwood, 1977; Farner, Follett, 1979; Wingfield, Farner, 1980). Conversely, decreasing day length in late summer could act as predictive information for termination of reproduction as appears to be the case in pigeons of the genus Columba (Lofts et al., 1966; Lofts, Murton, 1968) and possibly also the Baya Weaver, Ploceus philippinus, (Thapliyal, Saxena, 1964). However, most passerine species that breed in northern latitudes undergo spontaneous gonadal regression in mid-summer despite continuing long days which in spring were responsible for the stimulation of gonadal development. This photorefractory condition can also be induced by long days, and when in this state no known photoregime will stimulate gonadal recrudescence. The number of long days required to induce photorefractoriness is a function of day length (Dolnik, 1976; Farner, Gwinner, 1980; see also Moore et al. this volume) and in the White-crowned Sparrow, Zonotrichia leucophrys gambelii, the gonads will remain regressed for at least many years if maintained on permanently long days (Farner, Follett, 1979; D.S. Farner, R.A. Lewis, R.S. Donham, unpublished). Recovery of photosensitivity usually occurs only after birds have been exposed to short days for 40-60 days (Wolfson, 1952; Lofts, Murton, 1968; Turek, 1972, 1978; Dolnik, 1976; Farner, Follett, 1979). Under natural conditions, photosensitivity is regained in late October and early November when day length is still decreasing. Gonadal recrudescence is thus prevented until days lengthen the following spring (Farner, Mewaldt, 1955).

There is much evidence that an endogenous circadian rhythm is involved for measurement of day length, although the underlying mechanisms remain

obscure (for reviews see Farner, Follett, 1979; Farner, Gwinner, 1980; Follett, Robinson, 1980; Follett, 1981). Furthermore, it has also been demonstrated that Zonotrichia continue to measure day length in relation to recovery of photosensitivity (Turek, 1972). Curiously, the eyes do not appear to be involved, and the presence of photoreceptors in the basal hypothalamus has been implicated (Benoit, 1964; Menaker, Keatts, 1968; Yokoyama, Farner, 1976). In the Chukar Partridge, Alectoris graeca, the eyes are also not necessary for induction of photorefractoriness, or recovery of photosensitivity (Siopes, Wilson, 1978).

This type of photorefractoriness is by no means common to all species investigated. In some the recovery of photosensitivity may not be dependent upon short days, e.g. Starlings, Sturnus vulgaris, (Schwab, 1971; Rutledge, 1974), and House Sparrows, Passer domesticus (Farner et al., 1977). In the House Finch, Carpodacus mexicanus, photosensitivity is recovered by exposure to a day length shorter than that required to induce photorefractoriness, but not necessarily shorter than the threshold day length required to stimulate gonadal development (Hanmer, 1968). In other species such as Mallards, Anas platyrhynchos (Lofts, Coombs, 1965), Japanese Quail, Coturnix coturnix (Follett, Robinson, 1980), and Bobwhite Quail, Colinus virginianus (Kirkpatrick, 1959), spontaneous gonadal regression occurs after exposure to long days, or as day length begins to decrease in mid-summer, but subsequent exposure to even longer days can induce gonadal recrudescence. In the Red-billed Quelea, continual exposure to long days eventually results in gonadal regression that is followed by spontaneous gonadal development (Lofts, 1962). However, as this species lives in equatorial Africa where there is virtually no annual photocycle, these results are difficult to interpret.

There is now compelling evidence for endogenous circannual rhythms of gonadal growth and regression in several avian species (e.g. Phylloscopus, Sylvia and Sturnus), and these rhythms are entrained by day length, or other factors, into cycles of exactly one year (e.g. Berthold, 1977; Gwinner, 1975, 1981; Farner, Gwinner, 1980). This mechanism is particularly attractive for migratory species that winter in equatorial regions where photoperiodic cycling is absent, or for transequitorial migrants that are exposed to long days on their wintering grounds, e.g. the Short-tailed Shearwater, Puffinus tenuirostris, (Marshall, 1959, 1960; Marshall, Serventy, 1959). In another transequitorial migrant, the Bobolink, Dolichonyx oryzivorus, photosensitivity is recovered on the shortening days during autumnal migration. On their wintering grounds in South America, these birds are exposed to day lengths of 14 hours, perhaps less. If photosensitive Bobolinks are subjected to 14 hours of light in the laboratory, gonadal growth does not begin for at least 10 weeks, whereas exposure to day lengths of 16 hours or longer will induce immediate recrudescence (Engels, 1969). The delayed response to 14 hour day lengths thus prevents premature gonadal recrudescence on the wintering grounds until about the end of March when the natural migration northward begins. Whether or not this delay in response to 14 hours of light represents some circannual component remains to be determined.

An additional hypothesis suggests that at least in the White-throated Sparrow, Zonotrichia albicollis, and House Sparrow, the annual cycle of mig-

ration, gonadal growth, refractoriness, and moult, is regulated by the phase angle between circadian rhythms of circulating levels of corticosterone and prolactin which are themselves entrained by day length, and possibly other factors such as ambient temperature (for reviews, see Meier, Ferrell, 1978; Meier et al., 1980).

Changes in the endocrine system that accompany photoperiodically induced gonadal growth and regression may also play some role in development of photorefractoriness. In Willow Ptarmigan, Lagopus lagopus lagopus, Red Grouse, L.l.scotticus, and Mallard there is evidence for an increase in the sensitivity of the hypothalamus to gonadal steroid feedback so that even very low circulating levels of sex steroid hormones are sufficient to suppress secretion of gonadotrophins (Sharp, Moss, 1977; Sharp, 1980; Stokkan, Sharp, 1980a; Haase et al., 1982). A similar hypothesis has been proposed for Z.l.gambelii (Matt, 1980) and for P.philippinus (Singh, Chandola, 1981) although the latter authors suggest that gonadal steroids may also increase the threshold day length required for a photoperiodic response thus resulting in gonadal regression. These data are supported by the observation that implants of an androgen blocker, cyproterone acetate, into the basal hypothalamus prevents spontaneous gonadal regression in photostimulated Tree Sparrows (Cusick, Wilson, 1972). However, plasma levels of testosterone and dihydrotestosterone are basal in photorefractory Z.l.gambelii (Lam, Farner, 1976; Wingfield, Farner, 1978, 1980) and are similar to those of castrated males (McCree-ry, Farner, 1979). If the hypothalamus of Z.l.gambelii does become sensitive to very low levels of sex steroid hormones, then these levels are below the sensitivity of our assay systems (30-40 pg/ml) and in castrates are presumably of adrenal origin. Furthermore, unlike the situation in Lagopus and Anas, castration of photorefractory Serinus and Zonotrichia does not result in an increase in plasma LH until photosensitivity is regained (Nicholls, Storey, 1976; P.W.Mattocks Jr., pers. comm.). Nevertheless, changing sensitivity to feedback may interact with other direct effects of day length to "fine-tune" gonadal regression, or may represent an adjustment of the hypothalamo-gonadotroph axis from a state of high activity during reproduction to one of much lower activity during autumn and winter.

SITE OF PROTOREFRACTORINESS

It is now over four decades since the first detailed descriptions of photorefractoriness in the House Sparrow (Riley, 1936) and the European Redstart, Phoenicurus phoenicurus (Schildmacher, 1938), and yet it is still not clear which component or components of the central nervous and neuroendocrine control systems are involved. The possibility that the gonads become refractory to the actions of gonadotrophins has been ruled out since injections of mammalian luteinizing hormone (LH) and follicle-stimulating hormone (FSH) stimulate gonadal growth in photorefractory Z.l.gambelii (Stetson et al., 1973), House Sparrows (Vaugien, 1955), and others (Riley, Witschi, 1938; Schildmacher, 1939; Miller, 1949). Moreover, Novikov (1955) demonstrated that testes of photorefractory House Sparrows grow quite normally if transplanted into photostimulated hosts.

More recently it has been shown that plasma levels of LH in castrated Z.l.gambelii decline spontaneously in mid-summer in the same manner as those of intact controls (Matthocks et al., 1976). Similarly in Tree Sparrows, Spi-zella arborea, subjected to artificial long days, plasma levels of LH decline spontaneously in castrates at the same time as intact controls (Wilson, Follett, 1974). In photostimulated Z.l.gambelii and Canaries, Serinus cana-rius, plasma levels of LH and FSH decline in castrates up to two weeks before those of intact birds (Nicholls, Storey, 1976; Storey et al., 1980; Wingfield et al., 1980), although in the former species, basal levels of LH and FSH in castrates are not attained until day 75 of photostimulation, the same time as intact sparrows. These data suggest that although the presence of the gonad is not essential for the development of photorefractoriness, testicu-lar factors may modify its timing. This led to a revival of the "exhaustion" hypothesis first suggested by Miller (1954) and Dolnik (1964), which asserts that during photostimulation, some component of the hypothalamo-hypophysial unit becomes depleted. In the absence of negative feedback from sex steroid hormones, levels of gonadotrophins in castrates are greatly elevated over those of controls thus leading to exhaustion of the gonadotrophs, or hypotha-lamic neurons that secrete luteinizing hormone-releasing hormone (LHRH). Wing-field et al. (1979) demonstrated that intravenous injections of mammalian LHRH into male Z.l.gambelii elicited significant and approximately equal in-creases in plasma levels of LH in both photosensitive and photorefractory birds. McCarthy (1979) has confirmed and extended these findings to both male and female Z.l.gambelii, and essentially similar data have been presented for domestic ducks (Balthazart et al., 1980). Moreover, if castrated male Cana-ries (Storey, Nicholls, 1981), Z.l.gambelii (Matt, Farner, 1979), and Willow Ptarmigan (Stokkan, Sharp, 1980b) were given implants of testosterone in Si-lastic tubing, the photoperiodically induced rises in plasma LH were circulat-ing LH measured for several weeks further. With the exception of one group of Ptarmigan, LH levels increased after withdrawal of the implants and then declined as photorefractoriness developed at the same time as controls, and irrespective of when the implants were removed. In some groups, implants of testosterone were left in place until the controls had become refractory. Removal of the implants at this time did not result in an increase in plasma levels of LH indicating that these birds had also become refractory even though LH secretion had been suppressed throughout. These data argue strongly that the gonadotrophs of the anterior pituitary do not become refractory to LHRH, and argue against the exhaustion hypothesis.

Additional evidence comes from Erickson (1975) using an in vitro technique to measure release of gonadotrophins from adenohypophyses of cockerels by hypothalamic extracts of adult male Z.l.gambelii during artificially induced testicular growth and onset of photorefractoriness. The hypothalamic content of gonadotrophin-releasing activity increased dramatically after transfer to long days, began to decline 30 days later, and reached a nadir as photorefrac-toriness developed. Gonadotrophin-releasing activity remained low until photo-sensitivity was regained. Recently, R.A.Hudson, J.C.Wingfield, and D.S.Farner (unpublished) repeated these experiments in vivo. Hypothalami, and portions of cerebral cortex as controls, were collected from photosensitive and photo-

refractory male Z.l.gambelii and the tissue homogenized and extracted in 70% methanol at 0°C. Extracts were dried, taken up in 0.85% saline, and injected intravenously into photosensitive adult male Z.l.gambelii at a dose of 4 hypothalami per bird. Blood samples were taken at 0, 5, and 20 minutes after injection and plasma levels of LH measured. Neither saline alone, or extracts of cerebral cortex induced an increase in plasma LH. Hypothalamic extract from photosensitive birds increased circulating LH from 1.2 to 4.6 ng/ml within 5 minutes in a manner identical to that induced by injection of mammalian LHRH (Wingfield et al., 1979). However, hypothalamic extract from photorefractory birds injected into photosensitive sparrows did not induce any change in levels of LH consistent with the findings of Erickson (1975) that the hypothalamic content of gonadotrophin-releasing activity is low in photorefractory birds. Clearly these data support an hypothesis that photorefractoriness lies at the hypothalamic level or higher in the CNS, although the exact site remains to be discovered.

NON-PHOTOPERIODIC CONTROL OF REFRACTORY PERIODS

Although there appears to be no clear demonstration that birds become refractory to environmental stimuli other than day length, there is evidence that the onset of photorefractoriness can be delayed by non-photoperiodic information. Investigations of naturally breeding populations of Z.l.gambelii indicate that the timing of spontaneous gonadal regression is quite variable (Table 1). Unmated males become photorefractory in the fourth week of June, breeding males and females in the first week of July, and finally renesting birds, that had lost their first brood and initiated a second clutch in mid-June, were able to delay gonadal regression and onset of moult until the young fledged in the third week of July (Wingfield, Farner, 1978, 1979, 1980). Clearly it would be maladaptive for the parental phase of the reproductive cycle to be terminated abruptly since the young would not survive and the reproductive effort wasted. Rather, it appears that there would be selection for mechanisms that prevent the initiation of clutches beyond a certain date, but allow completion of a nesting phase that was initiated before this time. In the case of Z.l.gambelii, this period appears to be the third and fourth weeks of June (Wingfield, Farner, 1979).

The mechanisms by which photorefractoriness is delayed are by no means clear. It is possible that elevated circulating levels of sex steroid hormones during the initiation of a second clutch somehow delay gonadal regression and moult since testosterone has been shown to maintain a functional testis in Japanese Quail (Brown, Follett, 1977), and prevent spontaneous gonadal involution in photostimulated House Sparrows (Turek et al., 1976). Moreover, both testosterone and oestradiol delay onset of moult in Canaries (Kobayshi, 1952) and Z.l.gambelii (M.C.Moore, K.S.Matt, J.C.Wingfield, D.S.Farner, unpublished). Stimuli from the nest and eggs, or interactions between mates may also play a role, although data supporting such hypotheses are sparse. However, J.C.Wingfield and S.Runfeldt (unpublished) have shown that free-living female Song Sparrows, Melospiza melodia, (n=8) given subcutaneous implants of oestradiol in Silastic tubing, delayed gonadal regression and moult until at least the beginning of October. Control females

Table 1. Duration of maximum size (> 300 mg) of testes in captive and free-living Zonotrichia leucophrys gambelii*

| Treatment | Duration in days |
|---------------------------|------------------|
| Indoor cages (20L 4D) | 10 |
| Outdoor aviaries | 12 |
| Free-living, non-breeding | 25 |
| Free-living, breeding | 31 |
| Free-living, renesting | 44 |

* From Wingfield and Farner (1978, 1979, 1980).

($n=8$) given empty implants became photorefractory and began moult by mid-August, and all but 2 had vacated the breeding area by the end of August. Males mated to control females were also refractory by mid-August and most had left by early September. In contrast, males mated to oestradiol-implanted females did not become refractory and begin moult until late August to mid-September, up to one full month later than control males. Curiously, untreated females mated to males that had been given implants of testosterone ($n=9$) became refractory and began moult in mid-August, the same time as females mated to control males, even though testosterone-implanted males **remained on territory and delayed onset of moult until the beginning of October**. These data suggest that the male may "fine-tune" onset of photorefractoriness according to the reproductive state of his mate. Thus, it might be expected that unmated males would undergo gonadal regression before mated males (Wingfield and Farner, 1979; Table 1). On the other hand, females do not appear to fine-tune gonadal regression to the reproductive state of males. Presumably information from the nest and eggs, or young, provide additional sources of information for the female. Since prolactin is known to maintain parental behaviour in birds (e.g. Silver, 1978) it is tempting to speculate that this hormone may also delay onset of photorefractoriness. Partial support for this hypothesis comes from Kobayashi (1953) who found that prolactin delayed and interrupted the post-nuptial moult of Pigeons, Columba livia.

SUMMARY

In mid-summer many species of finches that breed at mid- to high-latitudes enter a photorefractory state during which the gonads undergo spontaneous regression. This state can also be induced artificially by treatment with long days. Current evidence suggests strongly that the physiological basis of photorefractoriness lies at the hypothalamic level or higher in the central nervous system. Under laboratory conditions the onset of photorefractoriness occurs rather synchronously among individuals. However, investigations of naturally breeding populations of Zonotrichia have demonstrated that unmated, non-breeding, birds enter the photorefractory state first, followed by nesting birds almost one full month later. This apparent plasticity in the timing of the onset of photorefractoriness allows completion of the

current nesting cycle rather than its termination before the young have fledged. Evidence suggests that stimuli from the nest and mate might play a key role in delaying onset of photorefractoriness, especially during re-nesting or late nesting attempts.

ACKNOWLEDGMENTS

Some of the investigations cited herein were supported by grants from the National Science Foundation to Professor Donald S. Farner, and by an allocation of the Biomedical Research Grant PHS RR 07065-15 to the Rockefeller University.

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THE PHOTOPERIODIC CONTROL OF AN ENDOGENOUS TIMER
REGULATING POSTNUPTIAL MOULT IN BIRDS

V.M.Gavrilov, I.N.Dobrynina

Department of Vertebrate Zoology of Moscow State University;
Institute of Evolutionary Morphology and Ecology of Animals of the
USSR Academy of Sciences, Moscow, USSR

The accurate timing of postnuptial moult to a definite season, the fixed pattern of relationship between moult and other periods of annual cycle, as well as synchronization of individual cycles during postnuptial moult, are suggestive of the moult being rigidly regulated by endogenous and exogenous factors.

In experiments, Zonotrichia leucophrys gambelia subjected in May to constant 20L:4D did not show any changes in the dates of postnuptial moult, while exposure to 8L:16D resulted in the absence of postnuptial moult for 400 days (King, 1968). In the same species subjected to 12L:12D, no moult was recorded for 46.5 months, although 2 to 4 growth cycles and gonad regression were noted (Farner et al., 1980).

Our studies in cooperation with V.R.Dolnik have demonstrated that an early onset of the spring state via exposure to longer photoperiods in winter and early spring results in an onset of postnuptial moult in the Chaffinch (Dolnik, Gavrilov, 1972; Gavrilov, 1974; Gavrilov, Dolnik, 1974; Dobrynina, Gavrilov, 1973; Gavrilov, Dobrynina, 1974; Gavrilov, 1977; Gavrilov, Dobrynina, 1977; Gavrilov, 1979; Dolnik, Gavrilov, 1980).

All the above evidence on the mechanisms of photoperiodic control of postnuptial moult in birds give grounds for proposing the following mechanisms of postnuptial moult in temperate-latitude birds:

1. Postnuptial moult is regulated by an independent photoperiodic system, which is developed not in all species.
2. Postnuptial moult is associated with hormonal changes caused by termination of sexual activity.
3. The onset of postnuptial moult occurs some time after the beginning of spring photostimulation, similar to the onset of photorefractoriness some days after the beginning of photostimulation.

We followed up our studies on the photoperiodic control of postnuptial moult in the Fringilla coelebs and extended our work to some other species differing in migration habits: the sedentary Passer domesticus and semi-sedentary Emberiza citrinella. In addition, the present communication includes the results of our study on photoperiodic regulation of the annual cycle in Otus scops, a nocturnal species.

MATERIALS AND METHODS

The study involved adult males (of three species as follows: Fringilla coelebs, Passer domesticus, Emberiza citrinella. For comparison, females were used, whose dates and rate of moult in captivity do not differ from those of males). The birds were exposed to daylength changes natural to the given locality. Beginning with a preset day, in groups of 5-10 individuals, the birds were placed in chambers with selected artificial daylengths. Using laparotomy, the size of testicles and postnuptial moult was assessed semi-

quantitatively (Dolnik, Gavrilov, 1974, 1980). To compare physiological properties of sedentary vs. migratory birds during moult, data on the annual cycles of some physiological indices are presented, some of which were published elsewhere (Gavrilov, 1974b; Gavrilov, Dolnik, 1976; Dobrynina, 1982; Gavrilov, 1983). The techniques for measurement of the histological and metabolic indices were described elsewhere (Dobrynina, 1982; Gavrilov, 1983).

In some cases the birds were autopsied, with testicles, ovaries and thyroid glands weighed and the brain fixed.

RESULTS AND DISCUSSION

In our earlier studies we have demonstrated that the dates of the onset of postnuptial moult are earlier the natural frist only in those groups of Chaffinches in which the onset of the spring breeding state was earlier induced (Dolnik, Gavrilov, 1972; Gavrilov, Dolnik, 1974; Gavrilov, 1974; Dolnik, Gavrilov, 1980). From numerous experiments we have inferred that the onset of postnuptial moult is regulated by a free course of circannual rhythm in relation to the spring action of photoperiod. The onset of postnuptial moult is not related to the initiation of spring photostimulation but to the completion of the unifactorial phase of photoperiodic control of the development of spring state, when the endogenous rhythm coincides with the astronomical calendar to the greatest extent. Through experimental photostimulation at different dates, as well as through exposure to different daylengths, and the duration of the unifactorial phase of photoperiodic control, the spring state can be reduced and caused to occur at earlier dates. Respectively, the dates of onset of postnuptial moult in these Chaffinch groups are shifted (Gavrilov, 1974; Dolnik, Gavrilov, 1980). The duration of moult was checked, using separate controls both for its initiation and termination.

In these experiments we registered indirectly the level of spring state through changes in the size of cloacal protuberance in males, but failed to obtain correspondence of the date of onset of postnuptial moult with the level of decline in sexual activity.

From the investigation of some new species and accumulation of data on the size of testicles, it was inferred that exposure to 18L:6D beginning with February 10 caused a earlier development of reproductive activity in all the species under study, as well as subsequent initiation onset of postnuptial moult (Fig. 1). It should be noted that the amplitude and duration of the early induced reproductive activity are lower in all the species under study than in those caused by natural photoperiodic changes (Fig. 1). Moreover, although an earlier photostimulation did not result in a level of reproductive activity similar to that caused by natural photostimulation, in all the species under study the initiation of an earlier postnuptial moult coincided with a decline in reproductive activity similar to that induced to the species under study by natural photoperiodic changes. For the Chaffinch, we have some additional data which indicate that exposure to different daylengths from February 10, showed different levels of reproductive activity and its different duration, but postnuptial moult was induced by a similar decline of reproductive activity in all the groups concerned (there are no data on moult rate available).

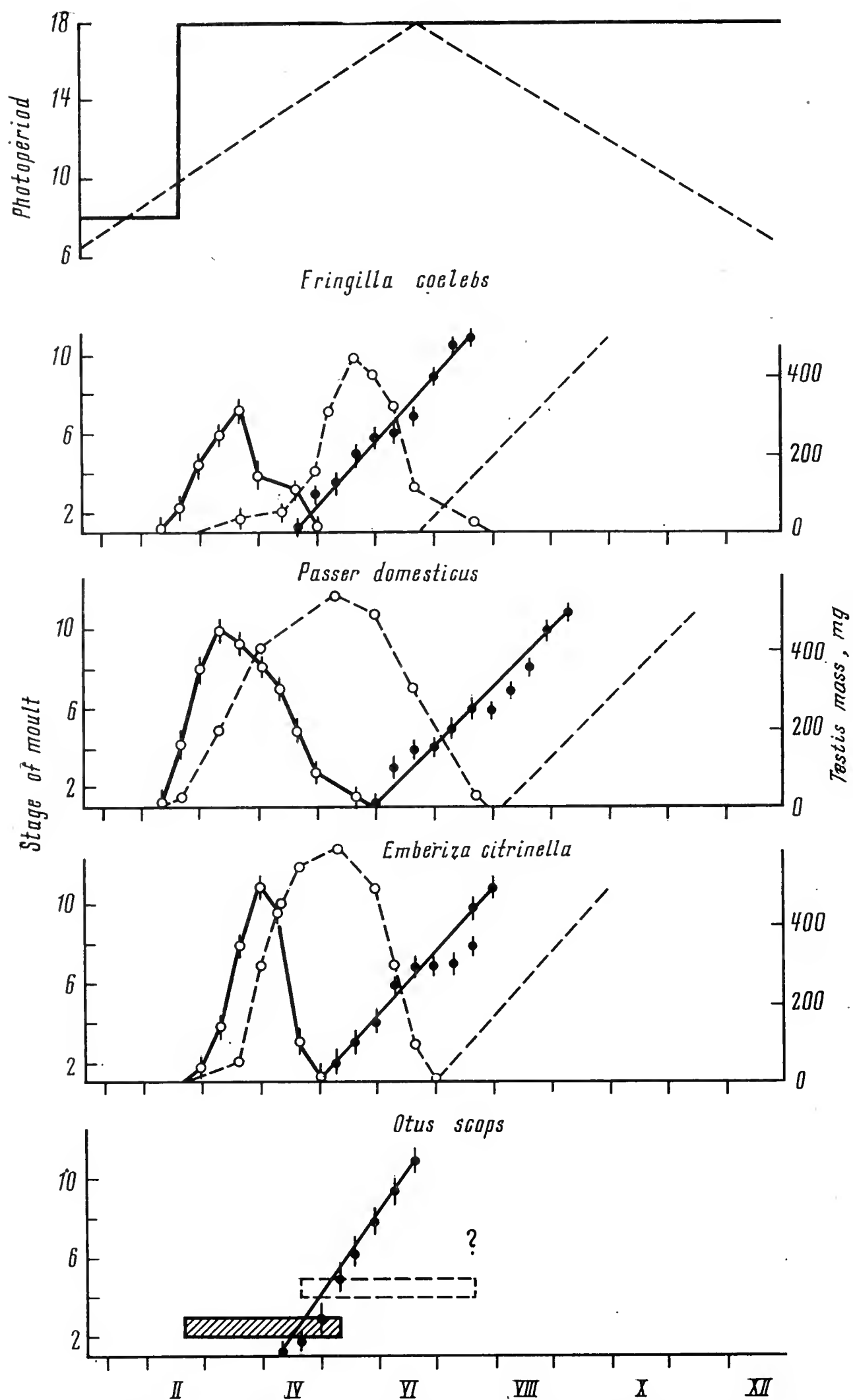


Fig. 1. Dates and stages of the moult of remiges (black dots and vertical lines) of artificially photoperiodic induced postnuptial moult (solid line), changes in the size of testicles (clear dots and vertical lines) under artificially photostimulation (solid line) and under natural photostimulation (dashed line) in species under study. Top, photoperiodic changes: solid line - artificially photostimulation, dashed line - natural photoperiod. In *O. scops*, instead of testicle size, the period of sex activity is given. Vertical lines at dots - standard error

Species-specific differences were revealed both in the rate of development of both reproductive activity and the rate of postnuptial moult (Fig. 1). The sedentary Passer domesticus and semi-sedentary Emberiza citrinella when stimulated by both early photostimulation and natural photostimulation, responded more quickly to photoperiodic changes, exhibited a more rapid gonadal growth, and the onset of postnuptial moult in them occurred at latter stages of the decline in reproductive activity (testicle weight 2-4 mg). In the Chaffinch gonadal growth was delayed by both artificially and still more so naturally increased daylengths, while the onset of postnuptial moult in them was initiated when the testicles attained a size of 100 to 130 mg. The duration and rate of early moult in all the species remained similar to those caused by natural daylength changes.

The maximal reproductive activity was attained: in Fringilla coelebs - 50 days after the onset of artificial photostimulations; in Passer domesticus - 30 days; in Emberiza citrinella - 40 days. These dates appear to be related to the manifestation (or non-manifestation) of migration state, but reliable data are lacking.

On the other hand, the time which elapsed between the maximal level of artificially induced reproductive activity and the onset of early postnuptial moult was 40 days in Fringilla coelebs, 90 days in Passer domesticus, and 90 days in Emberiza citrinella. Under natural photostimulation, this period is respectively 40, 90 and 50 days. The above indicates that both the earlier onset of reproductive activity and postnuptial moult, as well as natural photoperiodic changes in the species under study are closely interrelated and can be hardly separated in time.

Moreover, exposure to 6C:18D of F. coelebs and P. domesticus, beginning in late November and for 400 days, did not result either in initiation of reproductive activity or onset of postnuptial moult; hence, reproductive activity could not be experimentally separated from postnuptial moult in the above species. If the photoperiodic conditions of the experiment brought about the onset of reproductive activity, it was invariably followed by postnuptial moult, and inversely, non-initiation of reproductive activity corresponded to the failure of postnuptial moult to occur.

The F. coelebs experiments imply that on principle, as early as following the maximal level of reproductive activity, the rate of moult can be altered via a change in daylength (Table 1). In all cases, both when early moult was photostimulated and the Chaffinches were subsequently exposed to a shorter photoperiod, and when the birds were subjected to a shorter photoperiod at various states of reproductive activity up to the early stages of moult, the rate of moult changed in a similar pattern. A reduction in the photoperiod to 12 or 8 L at various stages of a natural reproductive cycle resulted in the postnuptial moult beginning somewhat earlier 7 days (on an average) compared with that in parallel groups maintained under longer photoperiods. A reduction of photoperiod on the days preceding the onset of postnuptial moult somewhat advanced the beginning of the moult, but no correlation between the date of the onset of postnuptial moult and duration of exposure to shorter photoperiods was recorded. At the beginning of moult, the rate at which the remiges passed moult stages and the index of regene-

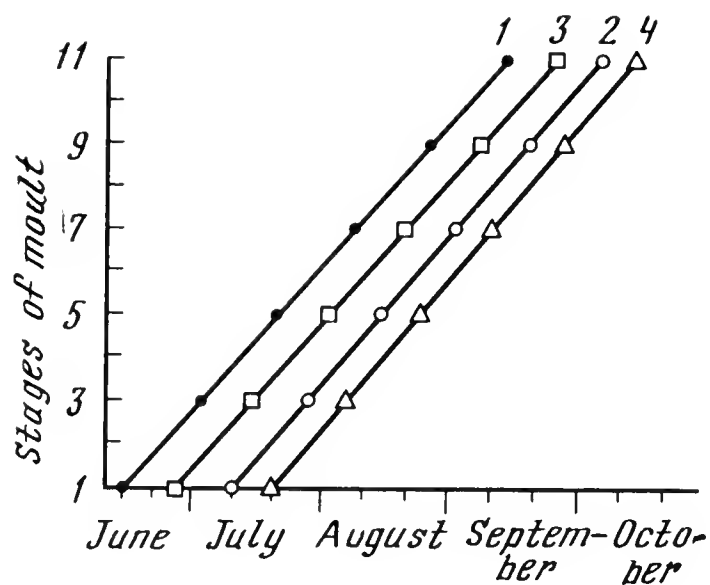


Fig. 2. Dates and stages of the moult of remiges in adult *F. coelebs* of different populations: 1 - northern population of *Fringilla c. coelebs* which moulted on the Kurische Nehrung, n=8; 2 - northern population of *Fringilla c. coelebs* which moulted in the north (Leningrad) n=6; 3 - population of *Fringilla c. coelebs* of the Kurische Nehrung, n=35; 4 - population of *Fringilla c. solomkoi* of the Grimea, which moulted on the Kurische Nehrung, n=6

ration of plumage under shorter photoperiods were much higher than in birds under longer photoperiods and in controls. That rate was higher at 8L:16D than at 12L:12D. After some time the rate of moult decelerated and terminated simultaneously with that in controls, and in the birds subjected to longer photoperiods. The change in the rate of postnuptial moult occurred under shorter photoperiods roughly during mid-moult as stage 5-6 of moult of the remiges. When the birds were exposed to a shorter photoperiod after the 5th stage of the moult of remiges, the rate of moult did not change compared with that of controls.

Thus, the moult rate between the 1st and 5th stages of the moult of remiges is regulated by the daylength, while the speedier postnuptial moult resulted in the shorter photoperiod (Table 1).

The above experiments have revealed that the time of the onset of postnuptial moult is dependent on spring photostimulation. It is noteworthy that the point of reference is not the entire photostimulation period, but some part of it (we shall refer to it as the late unifactorial phase of photoperiodic control of the development of spring state). Hence, if *F. coelebs* were placed at shorter daylengths beginning in winter through mid-May, the rate of their postnuptial moult did not differ from that in controls. In mid-May, Chaffinches arrive at their nesting sites, already at the peak of their reproductive activity. If we placed the birds at daylengths which were longer than natural, the first part of their postnuptial moult was characterized by the same speed as that in controls. But 30-45 days after the initiation of moult, when the birds attained stage 5 of the moult of remiges, the rate of moult began decelerating (Table 1), and the birds moulted for an indefinite period of time. In fact, some birds were still moulting as late as 30-70 and more days after the termination of moult in controls. Some of these birds, which were at stages 7 through 8 of the moult of remiges, were exposed to 12L:12D between October 11 and the time when the moult was terminated, i.e. after 40 days. Apparently, when stage 5 of the moult is attained, the cessation of moult control via shorter photoperiods initiates control of the postnuptial moult by longer photoperiods, which decelerates the moult rate.

As mentioned above, this type of control is only characteristic of the birds placed at a longer daylength, following the passage through the peak of reproductive activity under a shorter photoperiod. When the birds were maintained under a longer photoperiod and passed the peak of reproductive activity, no such effect was noted.

T a b l e 1. The effect of photoperiod duration and date of exposure to photoperiods on the rate and duration of moult in Fringilla coelebs

| Photoperiod conditions | Date of moult onset | Date of moult termination | Moult duration | Moult rate in first half of stage per day | Moult rate in second half of stage per day |
|------------------------|---------------------|---------------------------|----------------|---|--|
| Short light day | | | | | |
| 8L (from 1.06) | 15 June | 25 September | 102 | 0.714 | 0.063 |
| 12L (from 1.06) | 19 June | 25 September | 99 | 0.250 | 0.075 |
| 12L (from 24.06) | 27 June | 25 September | 90 | 0.250 | 0.083 |
| 8L (from 8.07) | 27 June | 25 September | 90 | 0.172 | 0.097 |
| 8L (from 5.08) | 27 June | 25 September | 90 | 0.122 | 0.122 |
| 12L (from 5.08) | 27 June | 25 September | 90 | 0.122 | 0.122 |
| Long light day | | | | | |
| 20L (from 1.06) | 27 June | 1 November | 127 | 0.120 | 0.069 |
| 20L (from 24.06) | 26 June | 28 November | 155 | 0.111 | 0.054 |
| 20L (from 8.07) | 27 July | - | - | 0.100 | - |
| 20L (from 5.08) | 27 June | 13 December | 170 | 0.122 | 0.046 |
| Control | | | | | |
| | 27 June | 25 September | 90 | 0.122 | 0.122 |

Presumably, the peak of reproductive activity, marks the daylength, which is the reference moulting photoperiod for the control mechanism at stage 5 of the moult of remiges. All the photoperiods longer than the one under which the peak of reproductive activity is passed will be regarded as long.

It should be noted that the handicapping effect of longer photoperiods manifests itself the longer the later the birds are exposed to it. The birds placed at a longer photoperiod in the middle of moulting, demonstrated the lowest rate of moult in its second half (Table 1). The termination of postnuptial moult in them was the latest. Thus, longer photoperiods in contrast to the shorter ones may affect the date of moult termination. Presumably, the same control mechanism switches off the shorter photoperiod control of postnuptial moult at that moment. Such a two-stage control of the postnuptial moult rate may ensure, firstly, through shorter photoperiods, and subsequently, through longer ones, similar dates of the termination of postnuptial moult in both birds that began moulting accelerate and those whose moult is delayed.

Geographical differences in the dates and rates of postnuptial moult were studied in four Chaffinch populations (Fig. 2). All the geographical populations of F. coelebs under study moulted at a similar rate, only the dates of postnuptial moult in different populations being different. Average dates were recorded for the population of the Kurische Nehrung of the Baltic Sea. A more northern population (Leningrad), which moulted in Leningrad, began

its postnuptial moult somewhat later. If a northern population is delayed in the south, its moult begins almost a month earlier than in its own range, and on an earlier schedule compared with Kurische Nehrung population, both populations moulting under the Kurische Nehrung photoperiodic conditions (Fig. 2). Southern populations appear to begin moulting somewhat later (at least, under the Kurische Nehrung photoperiodic conditions) than in the nesting range. Some fragmentary data on the moult of Fringilla coelebs solomkoi in the Caucasus are suggestive of an earlier moult under natural conditions (Gavrilov et al., 1979).

CIRCANNUAL CHANGES OF THE DATES OF REPRODUCTIVE PERIOD AND POSTNUPTIAL MOULT

Maintenance of the same birds under photoperiods at the natural investigation sites, led to an advance of the peak of reproductive activity in Chaffinches by 23 ± 4 days compared with that in the first year, and during the third year - by 28 ± 6 days compared with the first year. The dates of the onset of postnuptial moult changed by 26 ± 8 days during the second year compared with the first one, and by 24 ± 9 days compared with the first one ($n = 6$ during the first year; $n = 4$ during the second year; and $n = 3$ during the third year). The rate and duration of the postnuptial moult in these birds did not practically change in different years, being 94 ± 4 days during the first year, 88 ± 6 during the second year and 91 ± 7 during the third year.

400-day exposure of the Chaffinches to 6L:18D beginning with late November neither induced an increased development of gonads nor initiated postnuptial moult.

Otus scops which were maintained for 4 years under similar annual photoperiodic regimes also changed the dates of oviposition by 26 days, and the onset of postnuptial moult by 23 days (Fig. 3, 4). That species bred normally under laboratory conditions. Within the first two years, the reproductive period was discontinued at the oviposition stage, and during the two subsequent years the entire cycle was completed, including rearing of the nestlings. It is interesting to note that the completeness of the reproductive period did not affect appreciably the dates of subsequent postnuptial moult. The postnuptial moult could begin immediately after hatching, after rearing (Fig. 4) or even after the mating period (Fig. 1). In every case, a reduction in the period of reproductive activity and not postnuptial moult was recorded.

Unfortunately, we are lacking data on the course of seasonal phenomena in the same birds under natural conditions. Our experiments revealed that older birds exhibit earlier dates of reproduction and postnuptial moult. But under natural conditions, this feature may not be pronounced, since no great annual differences (about 1 month) were noted in older birds compared with the younger ones. In the wild, the reproduction cycle is to be related to that of environmental conditions, while the laboratory conditions are more stable and favourable (provided normal conditions are created). Thus, despite the fact that an earlier onset of reproduction is recorded in the wild,

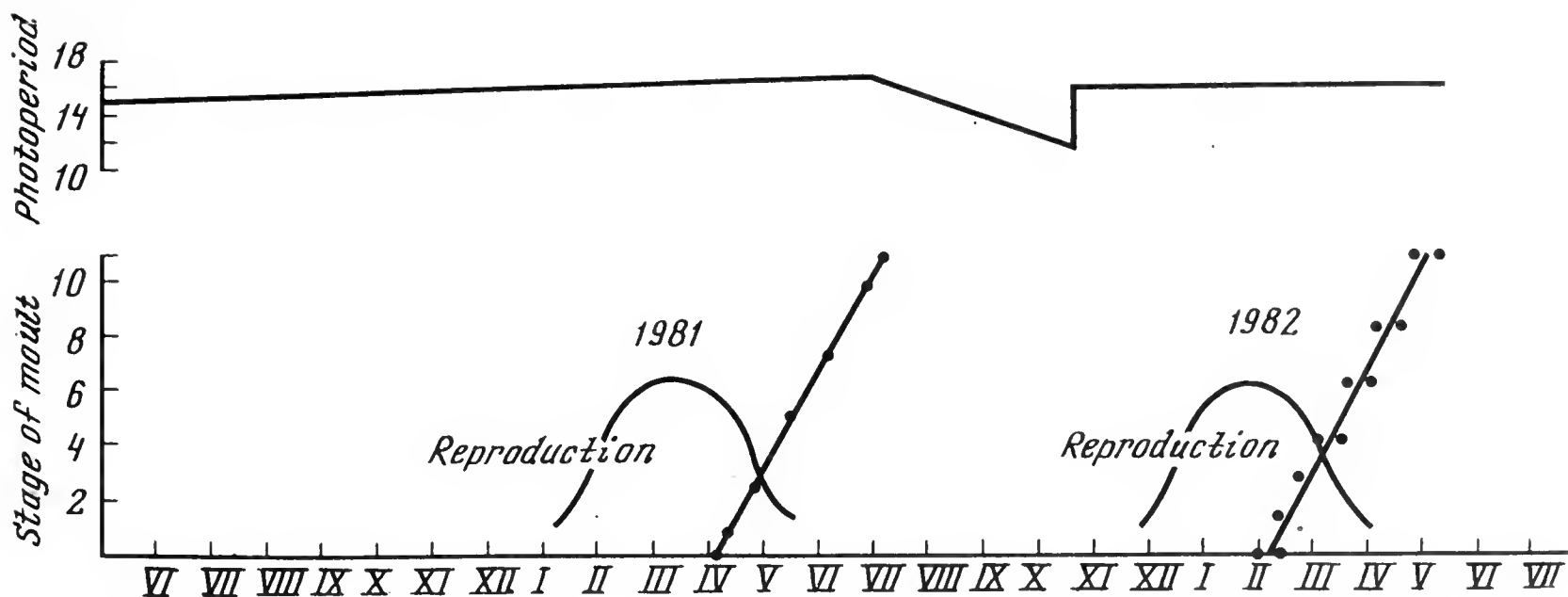


Fig. 3. Dates and stages of the moult of remiges (black dots) of the adult *Otus scops* under experimental photoperiods

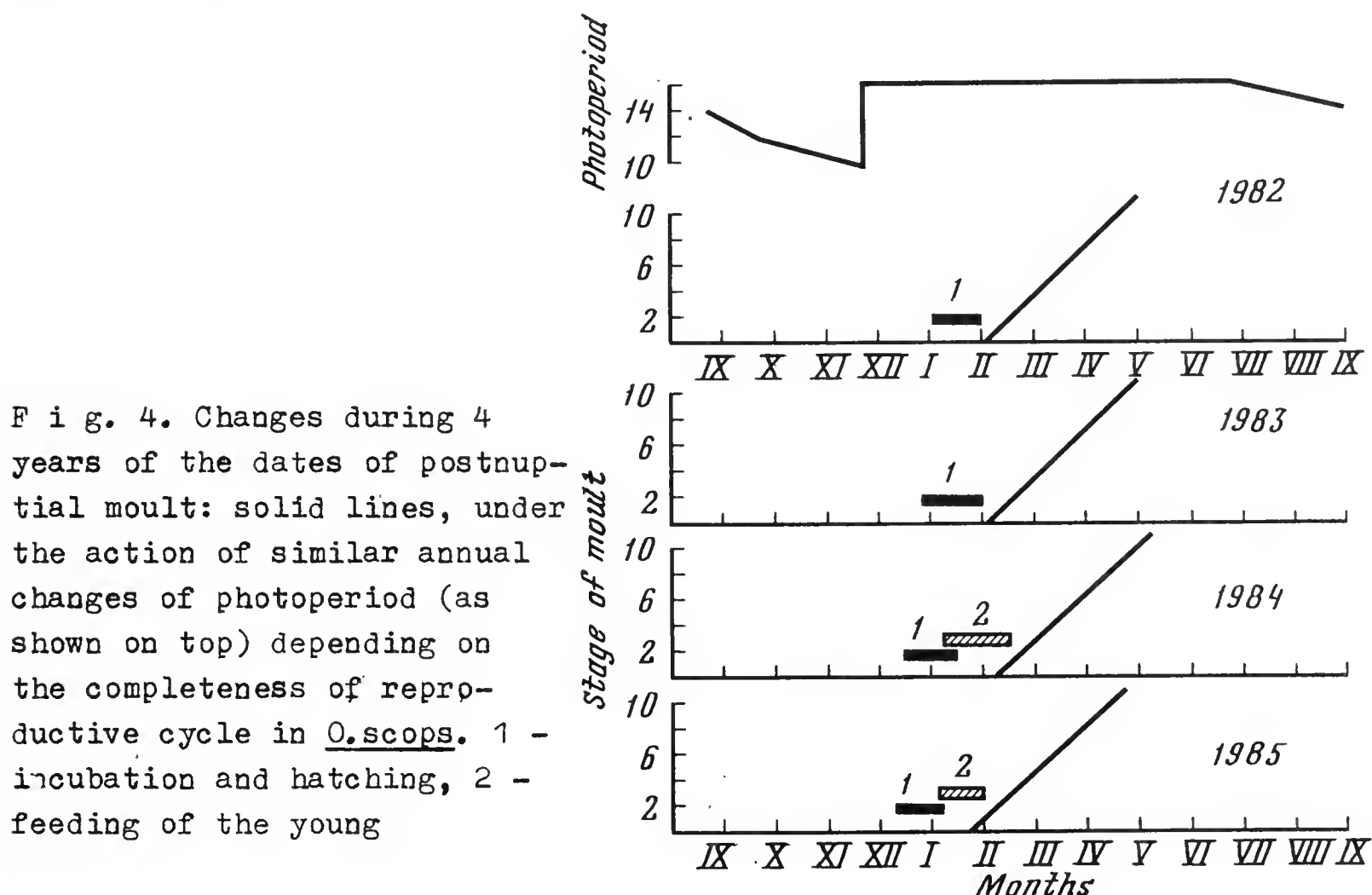


Fig. 4. Changes during 4 years of the dates of postnuptial moult: solid lines, under the action of similar annual changes of photoperiod (as shown on top) depending on the completeness of reproductive cycle in *O. scops*. 1 - incubation and hatching, 2 - feeding of the young

it is not highly pronounced in old birds. Nevertheless, the fact of circuman-
nual shifts of reproduction cycles and postnuptial moult both under natural
or stable artificial change of the photoperiod is, beyond doubt, provided
equal changes of the temperature and other environmental factors in the
laboratory.

THE CIRCUMANNUAL CYCLES OF PHYSIOLOGICAL INDICES

Comparison of the physiology of migratory and sedentary avian species
is primarily essential in the understanding the nature and regulation of the
migration state. But on the other hand, migration affects other phases of
the annual cycle: in many migratory birds, the postnuptial moult occurs more
rapidly than in sedentary, and the initial state of the gonadal growth in se-
dentary species is speedier in sedentary species than in migratory. We com-

pared some indices of the physiological state in the migratory F.coelelebs and the sedentary P.domesticus (Fig. 5). Differences in the weight and fat content cycles are largely associated with the onset or non-onset of the migration state. During the postnuptial moult, fat reserves are the lowest both in the sedentary and migratory species. The development of the spring process complex (growth of gonads in both species, migration behaviour in Chaffinches) coincides both in the Chaffinch and Sparrow with changes in the activity of the supra-optic nucleus of the hypothalamus (the volume of neurosecretory cells and of their nuclei decline). The supraoptic nucleus in P.domesticus is less pronounced morphologically, and its cell volume is smaller than that in F.coelebs. The circannual activity cycles in the paraventricular nuclei of the hypothalamus in both species are similar. During the spring period, the size of the cells and their nuclei decline, attaining the smallest/lowest values during the peak of gonad activity (Fig. 5), and the onset of moult corresponds to an increase in the size of the neurosecretory cells of this nucleus.

Under the effect of a longer photoperiod, a month-long period during winter, the activity of the supraoptic nucleus of Chaffinch changes sharply, while that of the paraventricular nucleus remains almost unchanged (Fig. 6). Premature photostimulation in winter induces the same changes in the activity of hypothalamus nuclei as natural photostimulation, i.e. the development of the complex of spring processes taking place against the background of a decline of the size in the neurosecretory cells of the supraoptic nucleus.

The circumannal cycles of activity of the thyroid as measured histologically differ in the species under study (Fig. 5). In the F.coelebs, the thyroid exhibits two pronounced activity peaks: in winter and during the postnuptial moult. In P.domesticus, the histological activity of thyroid has less pronounced peaks: during the reproductive period and during the postnuptial moult.

Under a month effect of a longer photoperiod during winter, the thyroid gland activity in the Chaffinch declines (Fig. 5). A prolonged effect of a lengthy photoperiod in summer (beginning on June 4) did not practically change the activity of the thyroid gland, while exposure to a shorter photoperiod at that time induced greater activity of the thyroid and also stimulated an earlier onset of the postnuptial moult (Fig. 7).

In spring, the sedentary P.domesticus shows a significantly earlier increase in the size of gonads than in the migratory F.coelebs (see Fig. 4). At the end of the spring period the rate of gonad development in the Chaffinch increases.

The effect of a longer photoperiod in winter did not result in the growth of gonads characteristic of spring either in the Chaffinch (Fig. 1, 6) or in the Sparrow (see Fig. 1). In the Chaffinch, the testicles increased to 185 mg a month, the ovaries - to 50 mg, and in the Sparrow, the weight of testicles was 440 mg after a month. The effect of a prolonged daylength in summer exerted practically no effect on the growth of testicles, while a shorter photoperiod somewhat accelerated the decline of gonads (Fig. 7).

Thus, the circannual cycles of activity of the thyroid glands in these two species differ. Apparently, the major function of the thyroid is metabo-

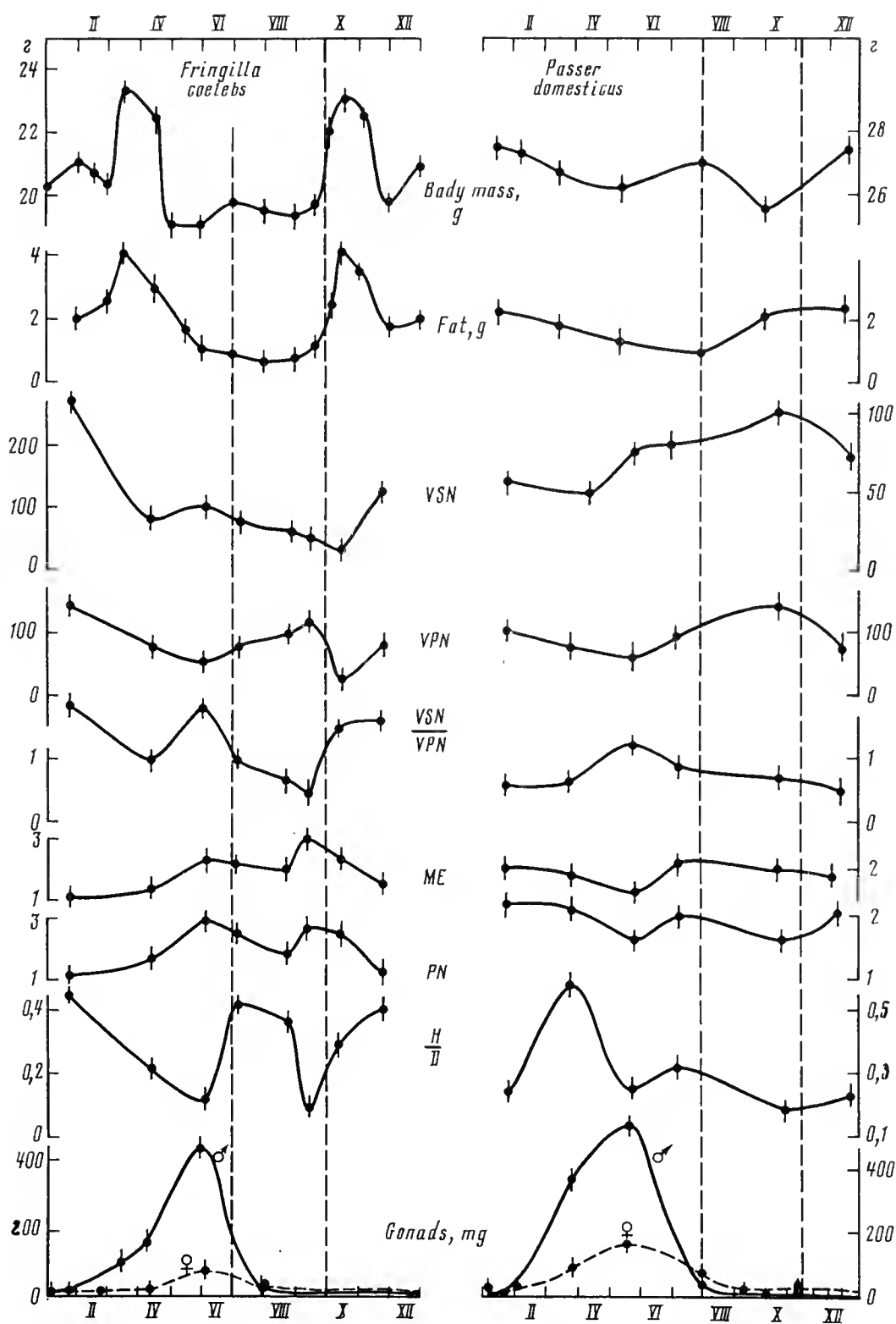


Fig. 5. Annual cycles of some physiological indices in Fringilla coelebs and Passer domesticus. Zone between dashed lines, period of postnuptial moult. VSN - Volume of the cell of the nucleus supraopticus. VPN - Volume of the cell of the nucleus paraventricularis. $\frac{VSN}{VPN}$ - Ratio of the volume of the nucleus supraopticus to the volume of the nucleus paraventricularis. ME - Neurosecretory material in the median eminence. PN - Neurosecretory material in the pars nervosa. $\frac{H}{D}$ - Ratio of epithelium's height to follicle's diameter of the thyroid's cells. Vertical lines represent the standard errors

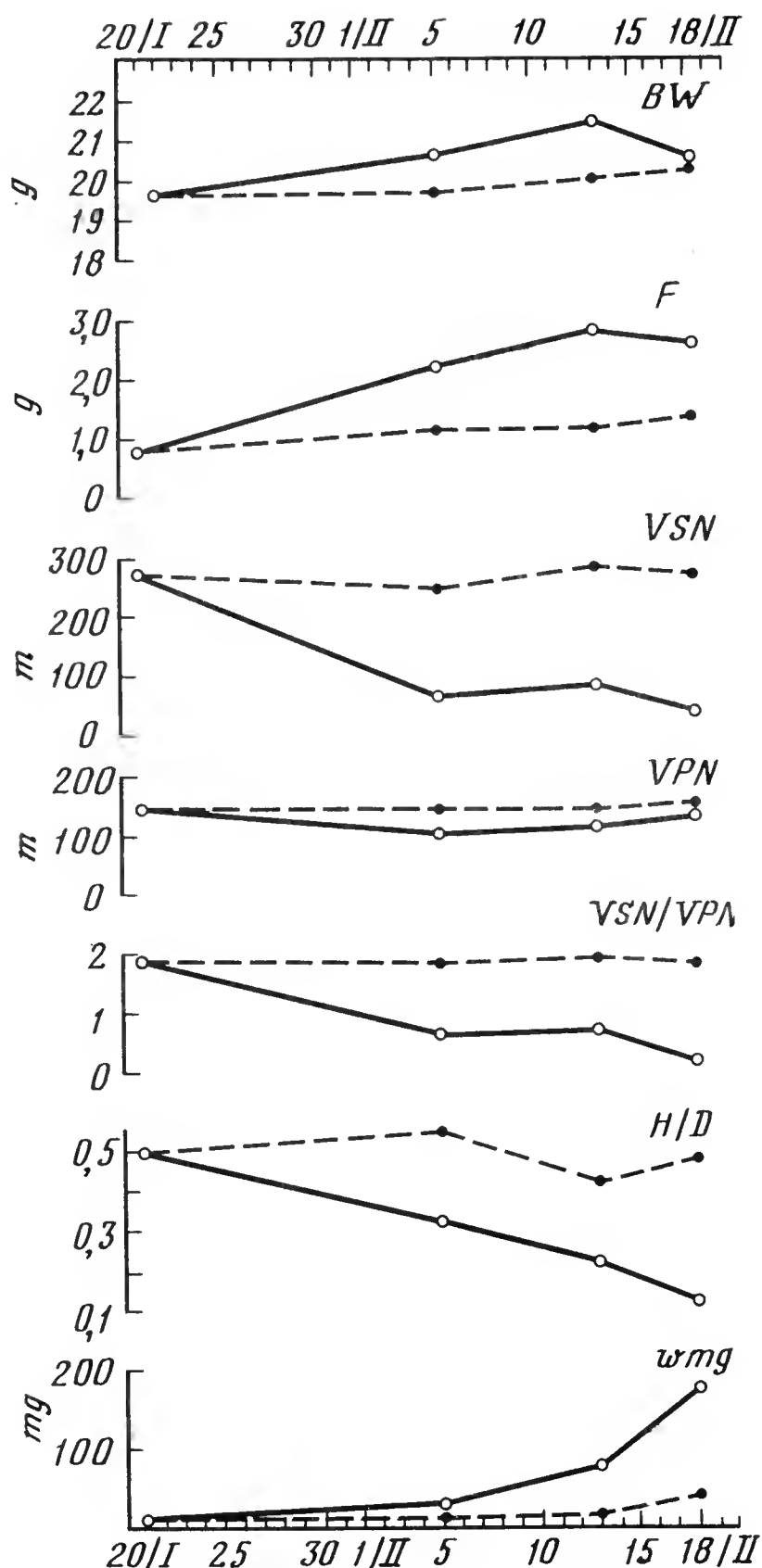


Fig. 6. The effect of the long photoperiod during a month in winter in *F. coelebs*. Designations as in Fig. 5. Dashed line-control. BM - Body mass, F - Fat, wmg - Weight of male gonads

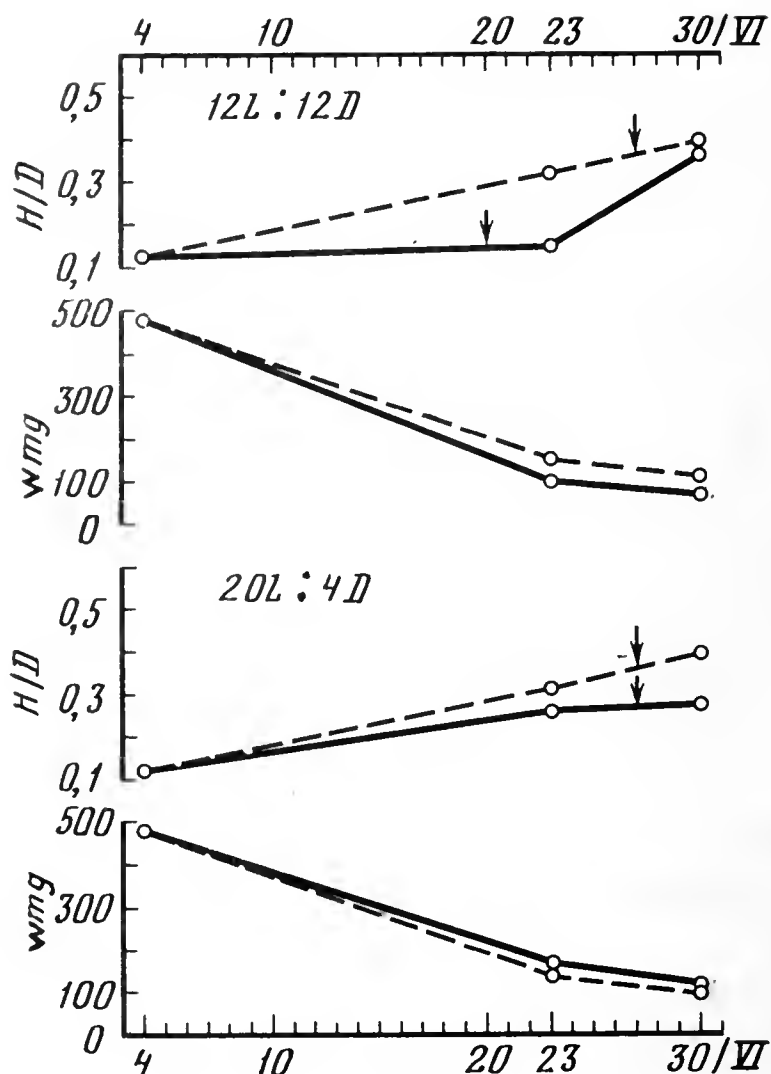


Fig. 7. The effect of the photoperiod 12L:12D (upper part of the figure) and 20L:4D (lower part of the figure) during a month in summer in *F. coelebs*. Designations as in Fig. 5. Dashed line-control. Arrows designate the onset of the postnuptial moult

lism regulation. In fact, the activity of thyroid gland in the species under study is well correlated to the circannual cycle of metabolized energy, with increased activity of the gonads preceding a higher rate of metabolism. The results of photoperiodic effect on the thyroid activity are suggestive of a circannual cycle of thyroid activity. In winter, exposure to longer day-lengths, somewhat increased the thyroid activity compared with the control birds. In summer, the thyroid activity is enhanced by longer photoperiods.

THE GENERAL PRINCIPLE OF THE OPERATION OF PHOTOPERIODIC REGULATORS OF POSTNUPTIAL MOULT IN SPECIES UNDER STUDY

All the species under investigation: Passer domesticus, Emberiza citrinella, Otus scops and Fringilla coelebs exhibited a relatively similar pattern of photoperiodic regulation of postnuptial moult. In all these species, the postnuptial moult is, directly or indirectly associated with the reproductive period, and we failed to obtain one of these processes experimentally. Hence, the results of our experiments on the photoperiodic control of postnuptial moult can be explained by an interaction of two factors as follows: endogenous circannual rhythm and the effect of photoperiod, following the postnuptial moult. Under the photoperiodic control of the annual cycle in spring, the endogenous rhythm is turned on, fixing the dates of onset and termination of the moult. The onset of postnuptial moult may occur in the species under study at different stages of the decline in then reproductive activity. After the programme for the date of postnuptial moult is incorporated in the endogenous rhythm (presumably during passage through the maximum of reproductive activity), an additional mechanism for synchronization of postnuptial moult in early- or late-moulting birds is turned on. In that case, a shorter photoperiod advances the onset and increases the rate of postnuptial moult - the shorter the photoperiod, the greater its effect. Under natural conditions, postnuptial moult occurs under decreasing daylengths. Hence, the role of daylength in the control of endogenous rhythm is the following. The individuals in which the moult programme is initiated endogenously at dates earlier than the time optimal for the population, the onset of postnuptial moult and its rate are slowed down by longer days. In individuals with retarded endogenous rhythm, a shortened photoperiod advances the moult. During the entire postnuptial moult, the effect of photoperiod is similar.

When birds are maintained under a short daylength at the beginning of the moult, when differences between natural and laboratory conditions are still great, the moult is advanced, and its development is far ahead of the endogenous rhythm programme. Because the course of moult deviates from this programme, the endogenous rhythm begins decelerating the course of moult. This deceleration is facilitated by the fact that during the experiment the difference between the natural daylength and photoperiodic conditions of the experiment is reduced. As a result, the dates of the termination of moult under shorter and natural daylengths are practically similar.

When birds are kept under constantly long days (in case the photoperiod is longer than that corresponding to the peak of reproductive activity), at the early stages of postnuptial moult, when the difference between the length of day and experimental photoperiodic conditions is small, the deceleration of the moult is negligible. During the experiment, the difference between the photoperiods increases, and, respectively, the impact of a longer photoperiod on the rate of postnuptial moult increases. Presumably, the date of moult termination is regulated by the endogenous rhythm individually, or more rigidly than the preceding course of the moult. In fact, the birds which, from the very outset moulted under 8L:16D, exhibited a repeated moult of some regimes at the end of the moulting period.

Such a photoperiodic control of the postnuptial moult is adaptive in terms of synchronization of individual cycles within the population with respect to environmental conditions. The control is non-adaptive when individual birds are transplanted to other geographical latitudes. Hence, the birds characterized by the above mechanism of postnuptial moult photoperiodic control should have inherent responses to daylength during the entire postnuptial moult.

Interestingly, at least two species F. coelebs and O. scops exhibited an increased sensitivity of the regulators to the action of photoperiod with age, due to which the cycle to follow is advanced.

Thus, our study has revealed that postnuptial moult may be initiated by spring photostimulation similar to photorefractoriness.

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EXOGENOUS AND ENDOGENOUS COMPONENTS IN THE CONTROL OF THE ANNUAL REPRODUCTIVE CYCLE OF THE EUROPEAN STARLING

Eberhard Gwinner, John Dittami, Gabriele Gänshirt,
Michael Hall, Joan Wozniak

Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell,
Radolfzell und Andechs, D-8138 Andechs, FRG

INTRODUCTION

During the past few decades endogenous circannual rhythms of various physiological and behavioral functions have been documented for a number of animal species. In birds, processes as diverse as molt, migratory unrest, gonadal size, and the preference for certain food stuffs may be under the control of such endogenous rhythms.

Whereas the adaptive value of these cycles in several avian species has been studied in considerable detail, relatively little has been learned about the physiological mechanisms by which they are generated (Berthold, 1974; Pengelley, 1974; Mrosovsky, 1978; Gwinner, 1981a,b, for reviews).

Circannual rhythms have been demonstrated in over 30 bird species. The annual cycles of many of these had previously been thought to be controlled by the seasonal variations in photoperiod. This has raised the question of how circannual rhythms and the photoperiodic control mechanism are related to each other (e.g. Aschoff, 1955; Farner, Gwinner, 1980). For a few species it has been shown that, on the level of a general oscillator model, the annual photoperiodic cycle can be considered a Zeitgeber, synchronizing an endogenously preprogrammed circannual rhythmicity (Gwinner, 1977, 1981a; Aschoff, 1980). This approach originated in the field of circadian rhythm research and uses the terminology developed in it. It has proven successful to the extent that it has led to a rather detailed description of the behavior of circannual rhythms under various environmental conditions and to an understanding of some formal properties of the system under both constant and varying photoperiods (e.g. Gwinner, 1975a, 1981a,b; Aschoff, 1980). On the basis of what has been learned from this formal analysis a more physiologically oriented approach seems now possible. The present paper summarizes the results of some experiments carried out with European starlings (Sturnus vulgaris) to investigate the way in which endogenous components and photoperiodic stimuli interact to produce circannual rhythms. Before proceeding to this discussion, some of the general properties of the starlings' annual rhythms of reproduction and other functions will be presented.

ANNUAL RHYTHMS UNDER NATURAL CONDITIONS

Figure 1 shows the seasonal changes of several physiological and morphological parameters of male European starlings held in Southern Germany in large outdoor aviaries. The birds go through a complete cycle of testicular recrudescence and regression in spring, which is paralleled by an increase and decrease in the plasma levels of LH and testosterone. Full spermatogenesis is attained when testicular width exceeds 5.5 mm (Schwab, 1971). Beak color changes from black to yellow due to androgen production, as the testes grow and then blackens again as the testes regress (Witschi, Miller, 1938). Following testicular regression the birds carry out a complete molt which

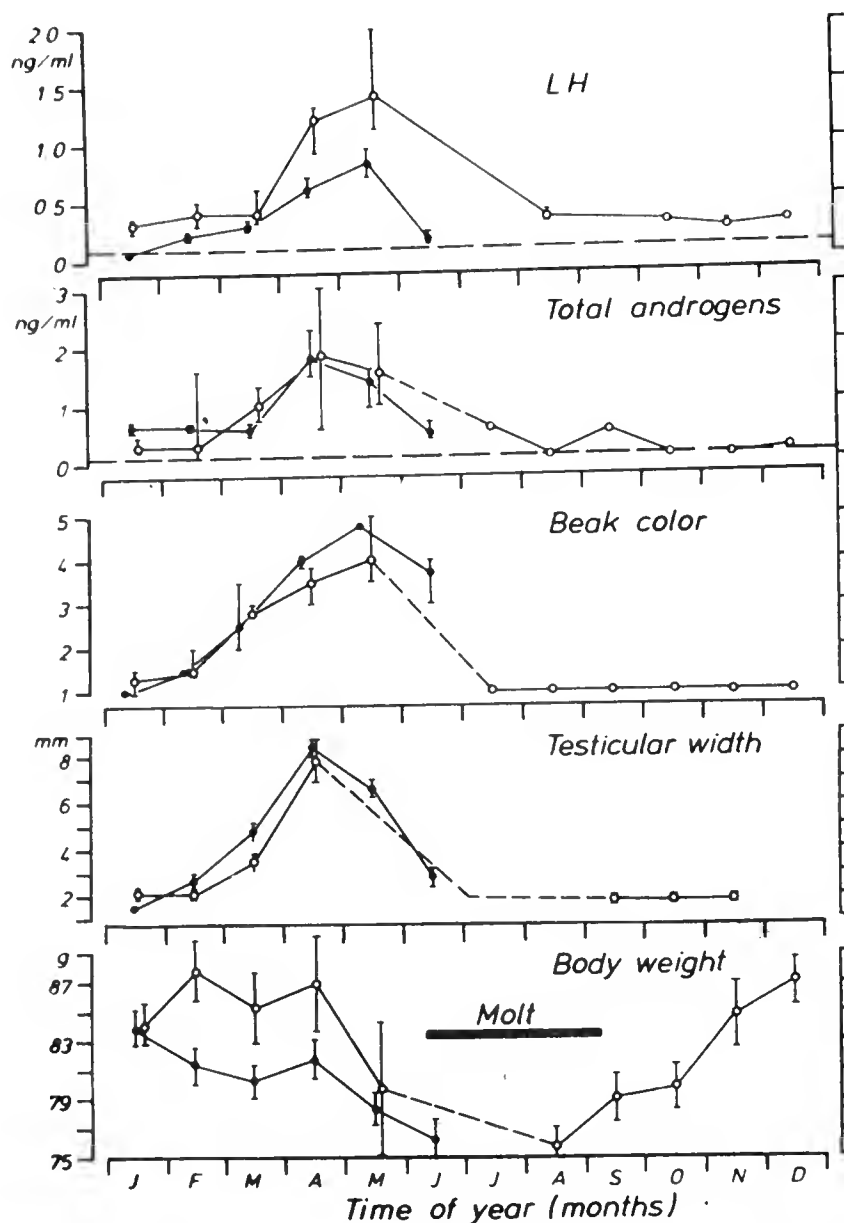


Fig. 1. Seasonal changes of body weight, testicular width, beak coloration, plasma-LH, and plasma-androgen content as well as occurrence of molt in two groups of male European starlings held in large outdoor aviaries in Southern FRG (48°N, 11°11'E). Closed circles: data from birds studied in 1978/79; open circles: data from birds studied in 1980/81. Both groups consisted of several subgroups which differed with regard to their social environment, and with regard to the availability of nestboxes but since only minor differences could be observed among the birds of these subgroups data have been pooled. Points in the curves for beak color, LH, and total androgens show medians with 95% confidence limits, points in the curves for body weight and testicular size show mean values with standard errors. They are based on data from 5 to 50 (in most cases 15 to 50) birds each. Testicular width was measured by repeated laparatomies of individual birds. The index of beak coloration was estimated on the basis of an index of 1 to 5; 1 characterizing an entirely black, 5 an entirely yellow beak (Gwinner, 1975b). LH and testosterone were determined by radioimmuno-assay. A purified chicken LH (AE-1) served as a standard as well as label and an anti-chicken LH (IRC/T) as an antiserum (Follett et al., 1972). Total androgens were measured according to Follett, Maung 1978. Dashed horizontal lines in the upper two graphs indicate the lower detectable limit of the radioimmuno-assays for LH and testosterone

usually begins around mid-June and extends through mid-September. Body weight also goes through a pronounced annual cycle with a maximum in early spring during the testicular growth phase and a minimum in mid-summer during molt.

EARLY PHOTOPERIODIC EXPERIMENTS WITH THE EUROPEAN STARLING

The photoperiodic control of these processes, particularly that of the annual gonadal cycle is well documented in the European starling. Indeed, the starling was an early model case for the study of avian photoperiodism. Bissonnette and Burger, in their classical work carried out in the 30s and 40s (summaries in Bissonnette, 1937; Burger, 1949), demonstrated the following: 1. Between late autumn and early spring long photoperiods stimulate gonadal growth. According to Burger the minimum photoperiod necessary for the rapid development of sperm is about 12 hours, but some testicular growth may take place in much shorter photoperiods (see also below). 2. This "progressive" phase is followed in late spring and early summer by a phase of testicular regression. Although regression may occur under many different photoperiods there appear to be qualitative differences between long and short photoperiods in the state of the testes after regression (Burger, 1947, 1949; see also below). 3. Following testicular regression under long photoperiods a state of photo-refractoriness ensues during which testicular recrudescence can no longer be reinitiated by long photoperiods. Under natural conditions this state extends from early summer through mid-autumn. It can be dissipated only by exposing the birds for some time to short photoperiods.

Although these early conclusions must be qualified and modified on the basis of more recent experimental work the general picture remains valid. From what had been learned in these early studies it was concluded that the overall form of the starling's annual reproductive cycle could be explained on the basis of the annual photoperiodic variations and the bird's seasonally changing responsiveness to them. "For the Starling, there seems to be no inherent gonadal rhythm which can act independently of external light changes" (Burger, 1949).

ANNUAL RHYTHMS UNDER SIMULATED PHOTOPERIODIC CONDITIONS

The important role of photoperiod for the control of the starling's annual gonadal cycle is further illustrated by the results of some more recent experiments in which starlings were exposed to artificial photoperiodic cycles of various shapes and frequencies, while other environmental variables were held constant. Figure 2 shows the behavior of 5 groups of male starlings which experienced photoperiodic cycles simulating those occurring at 5 different latitudes. The birds exposed to photoperiodic cycles of 67.5°, 60°, 42.5°, and 25° initially showed seasonal variations in testis size, bill coloration, body weight, and molt, similar to those observed in the aviary birds of Figure 1. However, differences between the various groups began to emerge at the start of the second gonadal cycle, after about 1 year of experimental conditions. This indicates that different photoperiodic cycles have modifying effects on the starlings' annual rhythms, although there seems to be some inertia in the response of the physiological mechanisms to the external stimuli (for a discussion see Gänshirt, Gwinner, 1979).

Instead of modifying the shape and amplitude of the photoperiodic cycle, its frequency can also be modified. Figure 3 illustrates changes in testicular size and molt in starlings which were held under sinusoidal photoperiodic

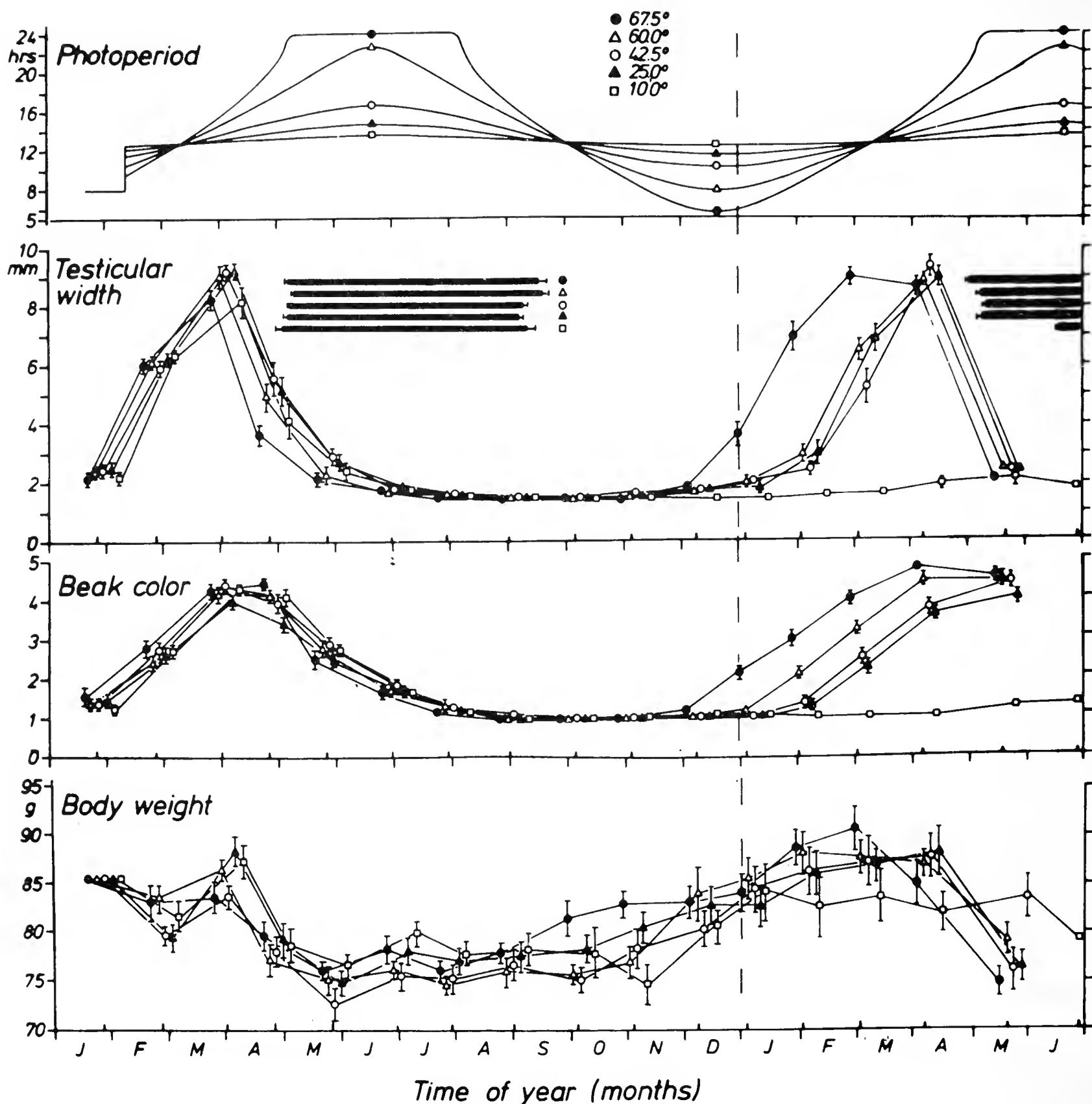


Fig. 2. Seasonal changes in body weight, bill coloration, and testicular width as well as occurrence of molt in 5 groups of European starlings ($N = 9-12$) exposed to photoperiodic cycles simulating those occurring at different latitudes (upper diagram). Points show mean values with standard errors of the means (after Gänshirt and Gwinner, 1979 and unpublished)

cycles. The changes simulated in general shape and amplitude, the cycle occurring at 40°N . However, the periods varied from 12 months to 1.5 months. In most instances the birds' testicular and molt rhythms followed the altered frequency of the photoperiodic cycle. Even cycles as short as 2, 1.7, and 1.5 months were capable of synchronizing these rhythms (although some deviations from the natural pattern occurred under these ultra-short photoperiodic rhythms; see Gwinner, 1981a for detailed discussion).

THE PATTERN UNDER CONSTANT PHOTOPERIODIC CONDITIONS

The results presented so far illustrate the significance of the annual photoperiodic cycle for the control of the starling's testis and molt

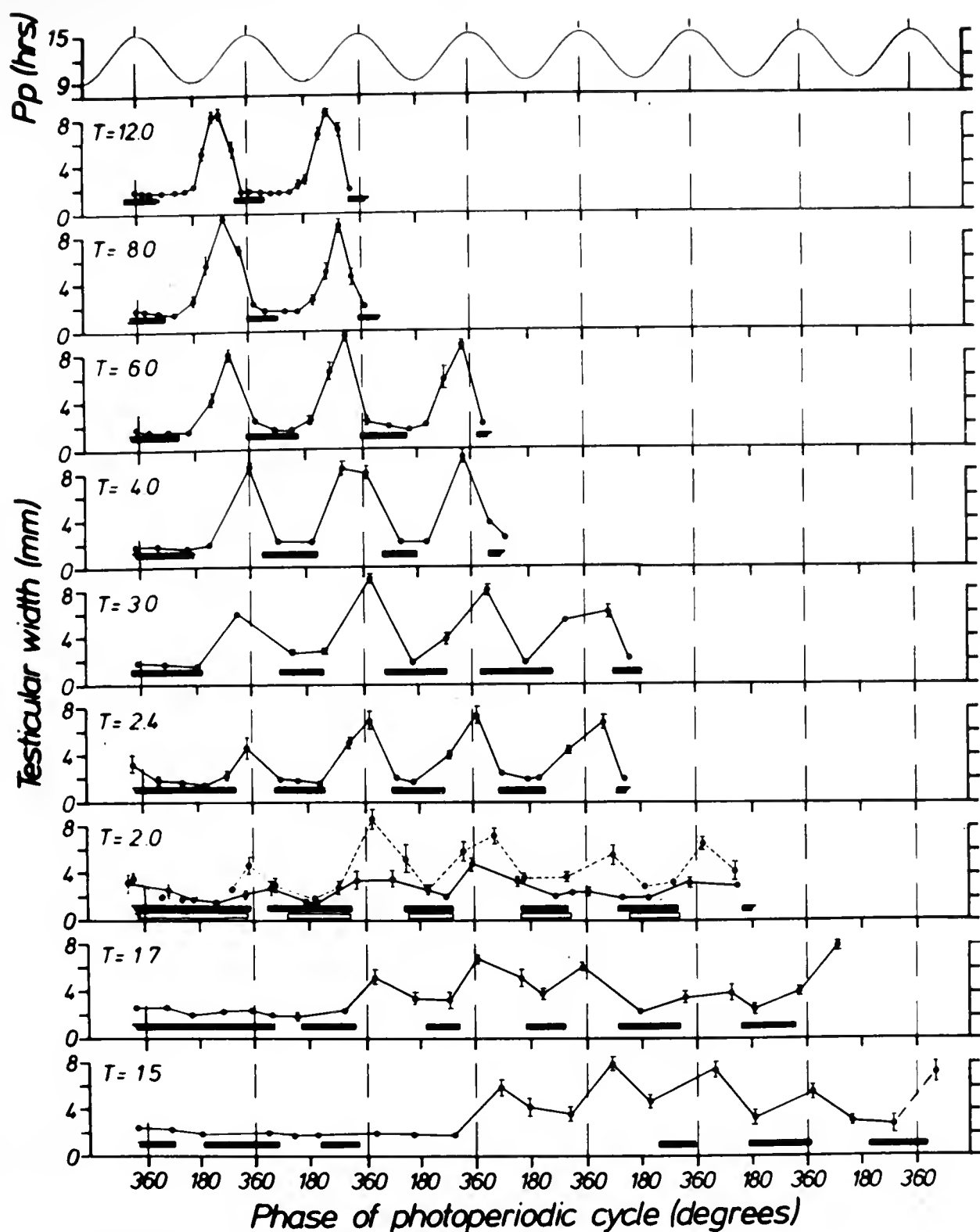


Fig. 3. Changes in testicular width and occurrence of molt in 9 groups of European starlings (consisting of 8 to 10 birds each) exposed to the sinusoidal changes of photoperiod shown in the uppermost panel. The amplitude and the general shape of these cycles were the same in all groups (and identical with those occurring at about latitude 40°) but their duration varied from 12 months (uppermost panel) to 1.5 months (lowermost panel). Points show mean values with standard deviations. Data are plotted relative to the phase of the photoperiodic cycle. Dashed vertical lines represent times of shortest photoperiod ("photoperiodic mid-winter"). Two experiments have been carried out under a photoperiodic cycle with 2 months duration (from Gwinner, 1981a)

rhythms. However, they are not sufficient to decide whether the annual photoperiodic cycle provides obligatory stimuli for the basic expression of these rhythms or whether it acts as a Zeitgeber on an endogenously preprogrammed rhythmicity. Figure 4 summarizes the results of experiments in which starlings were held for at least 6 months under a variety of different constant photoperiods. Only data from experiments which were initiated bet-

ween late October and mid-February, i.e. during the "progressive phase" are shown in this figure. Despite the fact that these data have been obtained from 3 different laboratories and with 2 different starling populations, a relatively uniform picture arises. The essential features derived from the experiments on Figure 3 and some additional studies can be summarized as follows:

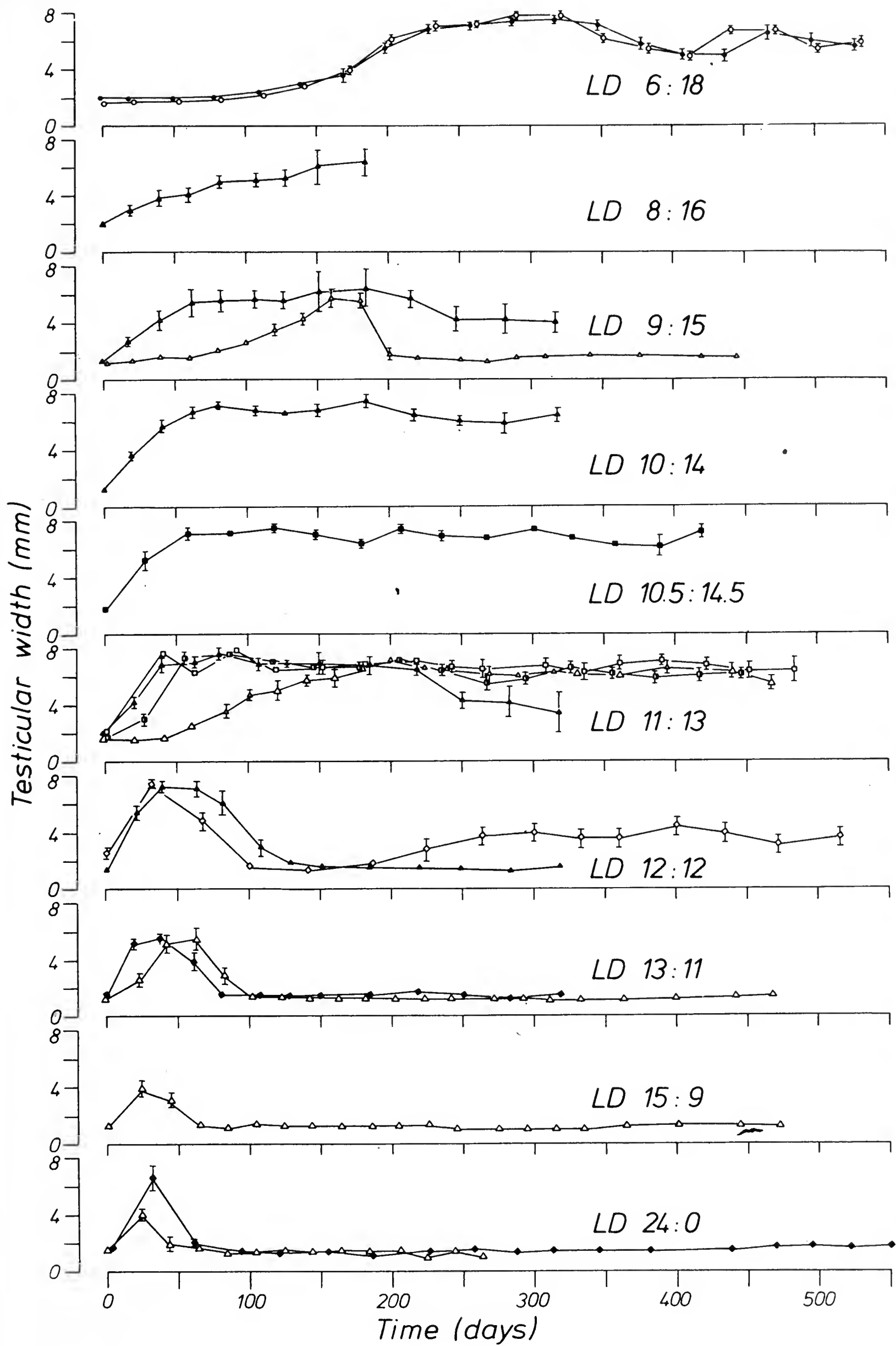
1. Testicular growth takes place under all conditions. The growth rate, however, depends on photoperiod. Between photoperiods of about 5 and 12 hours testicular growth rate increases with photoperiod but under photoperiods shorter than 5 hours the reverse may be true. In any case, full testicular maturation can be achieved under photoperiods as short as 1 hour (Schwab, Rutledge, 1978).

The testicular growth response to short photoperiods increases as the season progresses. Starlings exposed to a 6-h photoperiod in late January showed a greater testicular response than conspecifics exposed in October to a 4-h or an 8-h photoperiod, although, if measured simultaneously, the effectiveness of a 6-h photoperiod is normally between that of the 4-h and 8-h photoperiod (Gwinner, Gänshirt, 1982). This increasing responsiveness, which is also indicated by results presented by Schwab (1971) may explain why the testicular growth rates measured in the experiments of Hamner (1971; Fig. 4) tend to be smaller than those measured in comparable studies. Hamner's experiment started earlier than most of the others, in early November, possibly even while the birds were still in a state of relative photorefractoriness.

2. Under photoperiods shorter than 12 hours testes tend to stay large for a very long time. Data obtained on bill coloration in experiments under the 8-h, 9-h, 10-h, and 11-h photoperiod and on spermatogenetic activity in 2 experiments under a 6-h photoperiod indicate that the testes remain functionally active to the end of the experiments (Gwinner, Dittami, unpublished; Schwab, Rutledge, 1975).

It cannot be decided on the basis of the present experiments when or whether testicular regression under short photoperiods eventually occurs. Still, in 3 of 4 studies under the 11-h photoperiod no signs of testicular regression were observed up to the end of the experiments after about 15

F i g. 4. Changes in testicular width in groups of European starlings held for 6 months or longer under various constant photoperiods. Points show mean values with standard errors. Experiments were started between 26th October and 16th February. ● o: after Schwab, Rudledge (1975) start of experiments: 26th October (these experiments actually extended over 757 days, although only the first 530 days are shown here. ▲ after Gwinner, Dittami, 1982 and unpublished, start of experiment: 11th January. △ after Hamner 1981, start of experiment: 6th November. ■ after Schwab (1970), start of experiment: 22nd December. ▣ after Schwab (1970), start of experiment: 23rd November. □ after Schwab (1970), start of experiment: 19th January. ◇ after Gwinner, Dittami, 1980, start of experiment: 16th February. ◆ after Gwinner, Wozniak, 1982, start of experiment: 2nd January (LD 13:11), 14th January (LL)



months. In the fourth the testicular size of most birds eventually decreased significantly. The reasons for these differences are not clear. The same is true for the situation under a 9-h photoperiod. In Hamner's experiments an early and very rapid regression of the testes took place around day 200. In our own experiment, testes showed only a slight tendency to regress at a later stage. As in the variable results mentioned under (1) differences in the beginning of the experiment and/or the differential photoperiodic pre-history may be responsible but further experiments are required to clarify the situation.

A special situation was found under the 6-h photoperiod. In 2 replicate experiments carried out in successive years a decrease in testicular size was observed around day 300 followed by an increase about 3 months later. The same was also observed in individual birds (Schwab, Rutledge, 1975). A characterization of this trough is given below.

3. Under photoperiods longer than 12 hours testicular size goes through a rapid cycle, the duration and amplitude of which is an inverse function of photoperiod. Following regression testes remain small for up to 16 months and, as judged from bill coloration, inactive.

4. Under the 12-h photoperiod testes go through a cycle which is followed in most individuals by spontaneous testicular recrudescence. The small amplitude of the testicular curve during the second cycle is mainly due to the fact, that the individual birds initiated and terminated the second cycle at different times (Gwinner, Dittami, 1980).

In the starling such a circannual rhythm in gonadal size has also been found under an LD 11 : 11 (Gwinner, 1981c) and, in some individuals, in continuous dim light (Gwinner, 1973; Gwinner et al., 1981). Under normal 24-h light/dark cycles, however, it appears to occur only under a 12-h photoperiod, or under photoperiods very close to 12 hours. The properties of this circannual rhythmicity under such a 12-h photoperiod merit a more detailed description.

CHARACTERIZATION OF THE CYCLE UNDER A 12-h PHOTOPERIOD

As shown on Figure 5 a circannual rhythm in testicular size emerged under a 12-h photoperiod irrespective of when the experiment was initiated. The rhythms continued from the phase of the bird's annual gonadal cycle at which the transfer took place, with about the normal temporal pattern.

In contrast to some other species no truly long term experiments, extending over many years, have been carried out with the starling. The longest (43 months) studies have, nonetheless, indicated that circannual rhythms in gonadal size may persist without damping for at least 3 cycles. The intervals between successive testicular maxima and minima usually deviate from exactly 12 months attesting to the truly endogenous nature of this periodicity (Gwinner, 1981c).

It must be emphasized that not all individual birds held under a 12-h photoperiod exhibit clear circannual cycles as indicated for instance by the behavior of the birds depicted in the 2 lower graphs of Figure 6. A detailed description of the patterns which can be observed have been given elsewhere (Gwinner, 1981c).

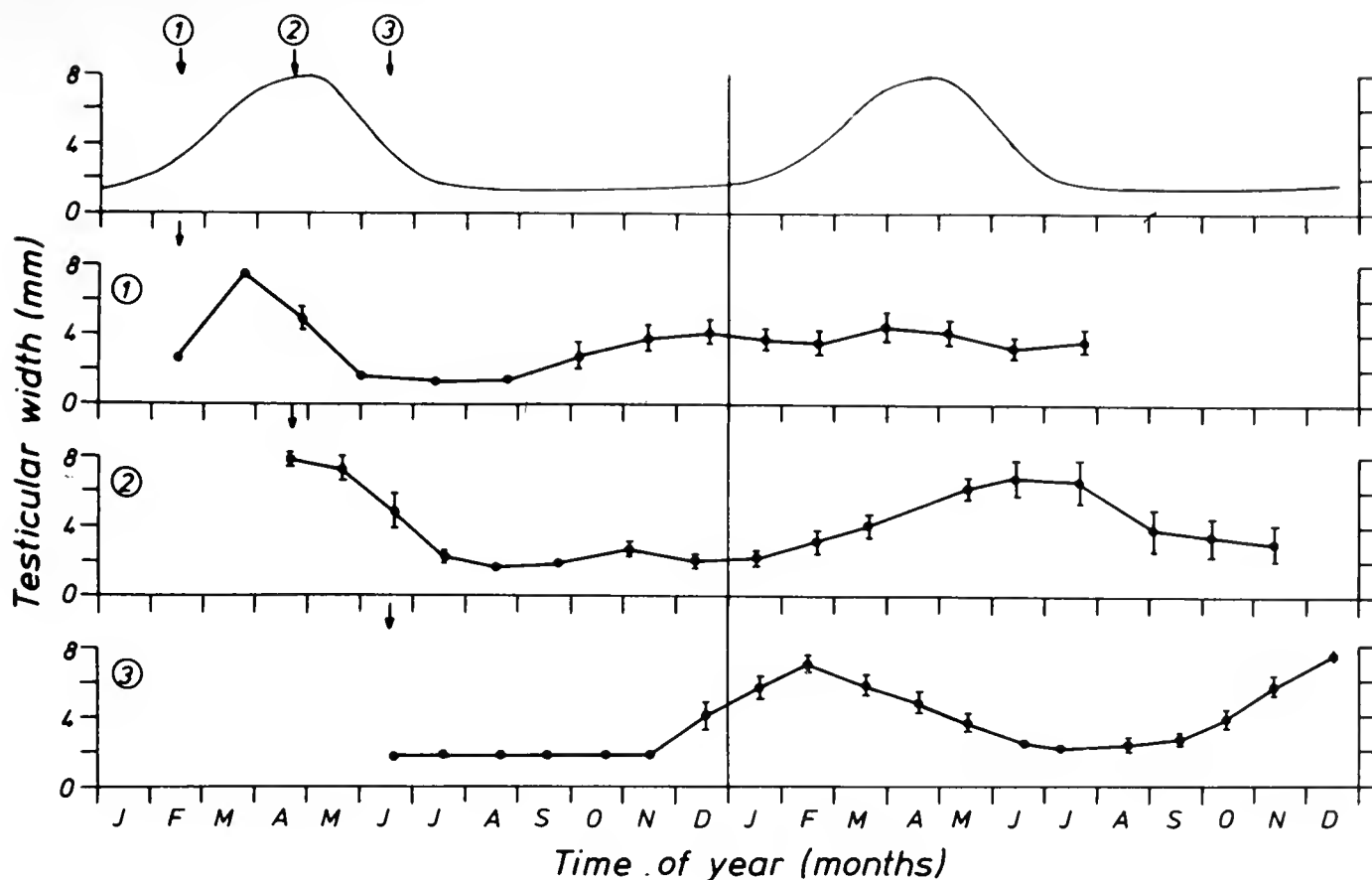


Fig. 5. Seasonal changes in testicular width of 3 groups of European starlings transferred at 3 different stages of their testicular cycle 1 , 2 , 3 -from natural photoperiodic conditions to a constant 12-h photoperiod. Points show mean values with standard errors. 1 -After Gwinner, Dittami 1980; 2 - after Gwinner (1981); 3 - after Schwab (1971)

The question may be asked whether those birds whose testes show regular cycles under a 12-h photoperiod go through the same stages of responsiveness to photoperiod as conspecifics under natural photoperiodic variations. In particular it would be interesting to know whether birds held under constant conditions enter a state of true photorefractoriness after testes have regressed. As Turner et al. (1980) have shown this is not the case in white-crowned sparrows (*Zonotrichia leucophrys*), whose testicular size exhibited periodic variations under a 12-h photoperiod. The results presented in Figure 6 indicate, however, that starlings kept under these conditions do become refractory. The testes of the 6 starlings in this experiment did not show any signs of growth when the birds were moved from a 12-h to a 20-h photoperiod after their testes had regressed. - The situation is very different in starlings whose testes size shows low amplitude variations under a 6-h photoperiod (Fig. 3). If exposed to a long 12-h photoperiod during the phase of partial testicular regression testes invariably developed rapidly to full size (Fig. 7) indicating that the quantitative differences in the shape of the curves for testicular size observed between the birds under the 12-h and 6-h photoperiod respectively are matched by qualitative differences in the underlying physiological mechanisms.

Although birds under a 12-h photoperiod do become refractory to long day stimulation this state dissipates with time as the testes eventually recrudescence. From histological studies and the changes in beak coloration it seems that during the subsequent testicular growth phase the testes eventually reach the same functional condition as those of freelifving conspecifics (unpublished observations).

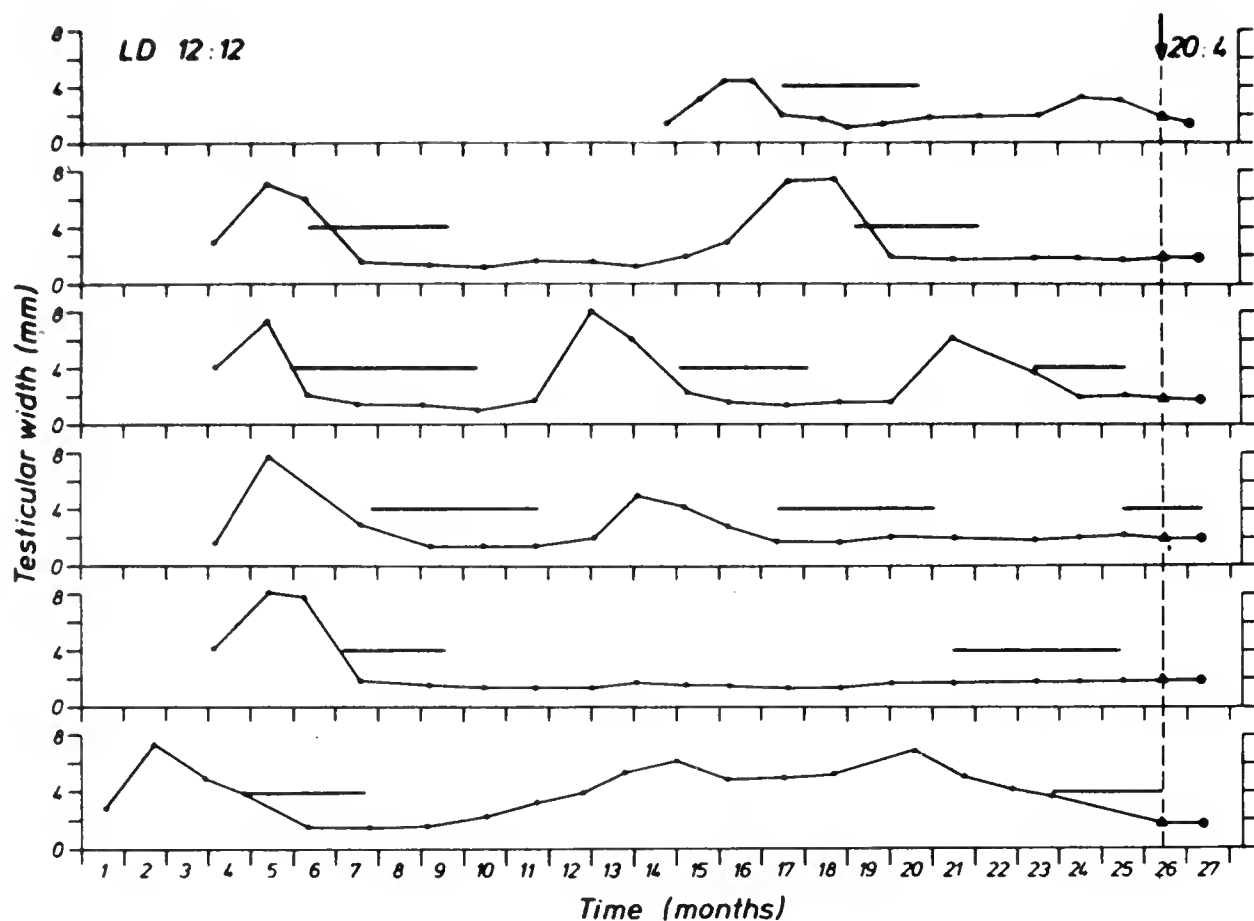


Fig. 6. Seasonal changes in testicular width in 6 individual European starlings held for 12 to 25 months under a constant 12-h photoperiod. At the time indicated they were transferred to a 20-h photoperiod and kept there for 25 to 32 days. After Gwinner et al. (1980)

WHY DOES RHYTHMICITY STOP UNDER PHOTOPERIODS LONGER AND SHORTER THAN 12 HOURS?

The fact that the circannual rhythmicity in gonadal size of European starlings persists under a 12-h photoperiod but not under daylengths longer or shorter than that, offers an opportunity for the study of the mechanisms that generate this rhythm in a 12-h photoperiod. By asking why circannual rhythms do not persist under long and short photoperiods we may find out why they do persist under a photoperiod in between. Specifically, 2 questions can be formulated: 1. Why is the starling's annual testicular rhythm arrested under photoperiods shorter than 12 hours, when testes are in an active state; and 2. why is it arrested under photoperiods longer than 12 hours, when testes are in an inactive state?

With regard to the arrest of the rhythm under long photoperiods after the gonads have passed through one initial testicular cycle, the hypothesis may be suggested that the second cycle is not initiated because photoperiods of more than 12 hours are too long to terminate photorefractoriness. This hypothesis is supported by the experiments summarized on Figure 8. Here birds whose gonads were in an inactive state after they had gone through a testicular cycle under a 13-h photoperiod (experiment 1) or in continuous bright light (experiment 2) were exposed for 19 to 55 days to a short 8-h photoperiod. When subsequently returned to the previous conditions their testes immediately grew. Obviously exposure to the short photoperiod had broken the birds' refractory state making them responsive again to the previously non-stimulatory long photoperiod.

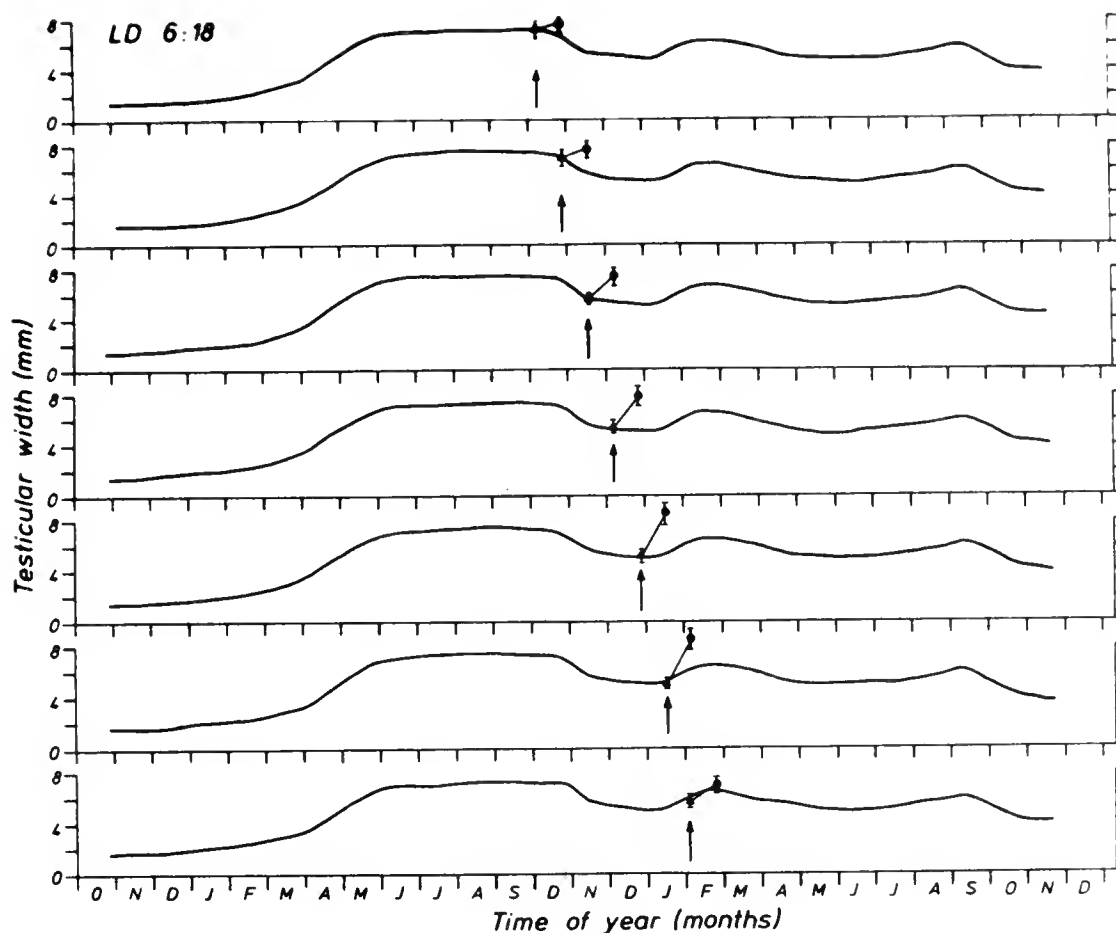


Fig. 7. The curves are a schematic representation - repeated 7 times - of the variations in testicular width of a group of starlings held under a 6-h photoperiod (Fig. 4 uppermost panel). At the times indicated by arrows subgroups of ten birds were removed from this group and kept for 20 days in a 12-h photoperiod. Triangles show the mean testicular width (with standard error) of the group continuing under the 6-h photoperiod at the times the transfers took place; dots show the mean testicular width of the subgroups after 20 days in the 12-h photoperiod. After Schwab, Rutledge (1975)

The hypothesis that photorefractoriness is not terminated under photoperiods longer than 12 hours has also been supported by an experiment carried out by Schwab (1980). Starlings were held under ahemeral photoperiodic cycle which, based on a 30-h light/dark cycle showed sinusoidal cycles with a minimum light time of 12 and a maximal light time of 18 hours. In contrast to birds held under naturally cycling photoperiods (see Figures 2,3) these birds never showed any testicular recrudescence.

With regard to the arrest (or considerable delay) of the rhythm under short photoperiods after gonads have grown, it seems likely that photoperiods less than 12 hours are too short for photorefractoriness to develop. Recent results in our laboratory have indeed shown that full testicular regression leading to a state of true refractoriness can be induced in birds held previously in an 11-h photoperiod, by any daylength of 12 hours or longer. Still, the picture is complicated by the fact mentioned already by Burger (1947, 1949) that regression can also be induced by photoperiods shorter than 12 hours. The type of regression under short days is, however, qualitatively different from that under long days in so far as the testes of the birds continue to produce testosterone, judging from the yellow bill coloration, and a state of photorefractoriness is apparently never attained.

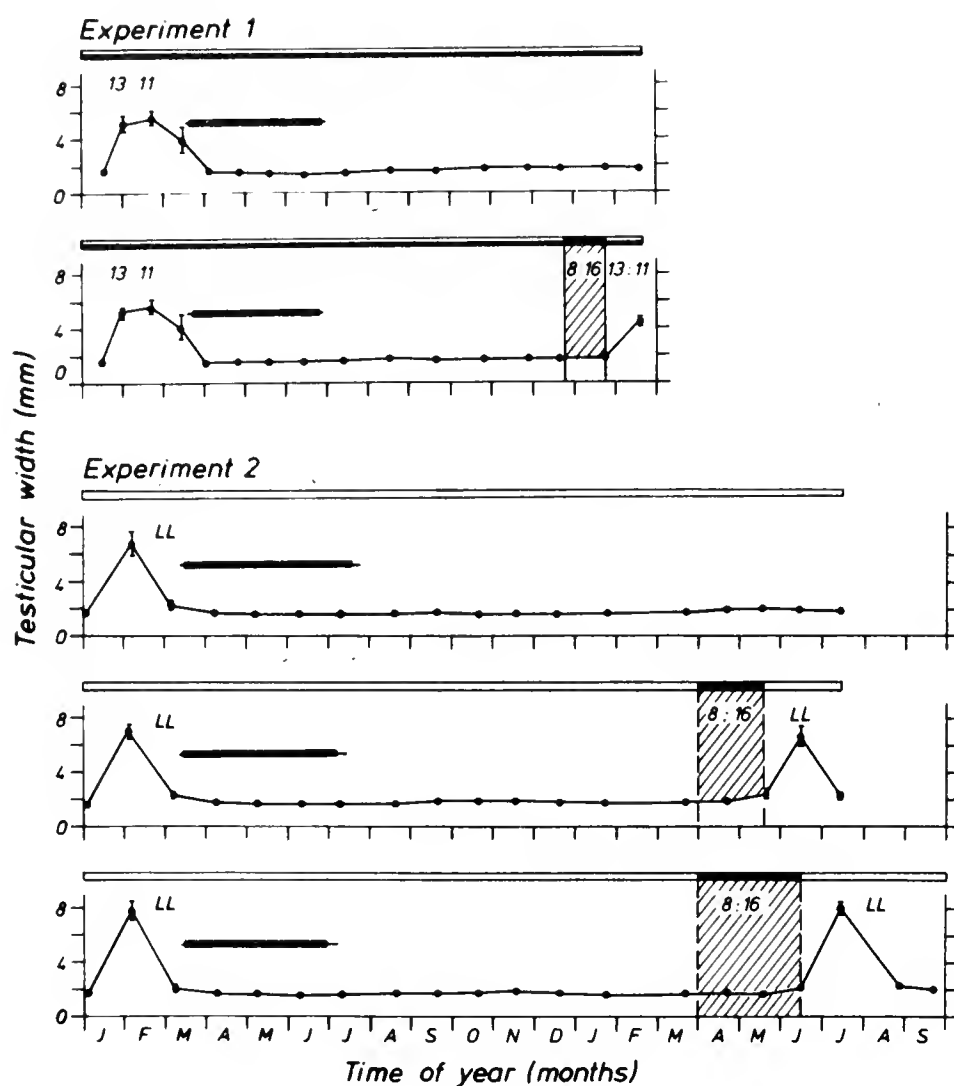


Fig. 8. Variations in testicular width (curves) and occurrence of molt (bars) of European starlings which were first held under a 13-h photoperiod (experiment 1) or under continuous bright light (experiment 2). During the times indicated by the shaded areas one group in experiment 1 and 2 groups in experiment 2 were exposed to an 8-h photoperiod before returned to the previous conditions. After Gwinner, Wozniak (1982)

A SCHEME FOR THE ENDOGENOUS AND PHOTOPERIODIC CONTROL OF THE STARLING'S ANNUAL REPRODUCTIVE CYCLE

On the basis of the results presented in the previous paragraphs, and some additional data, a tentative scheme for the starling's annual reproductive cycle can be proposed (Fig. 9). This scheme is partly identical with one previously proposed by Schwab (1971) and Hamner (1971) but expands several aspects of it. For the present purpose, we find it useful to distinguish between 2 successive stages in the cycle and to identify the spontaneous and photoperiodically modified processes occurring within them and during the transitions from one to the next.

Phase 1. Beginning around the time of the autumnal equinox, during the "progressive" phase, starlings develop an increasing tendency towards testicular growth. This increasing readiness occurs spontaneously (i.e. under a constant 12-h photoperiod) and eventually leads to full spermatogenesis under many and possibly all photoperiods. One of the consequences of this for the natural situation is that testicular recrudescence may begin as early as early January, when the photoperiod may still be less than 8 hours. In some populations like the British one, gonadal development may even begin before the winter solstice (Bullough, 1946). The tendency of the gonads to grow

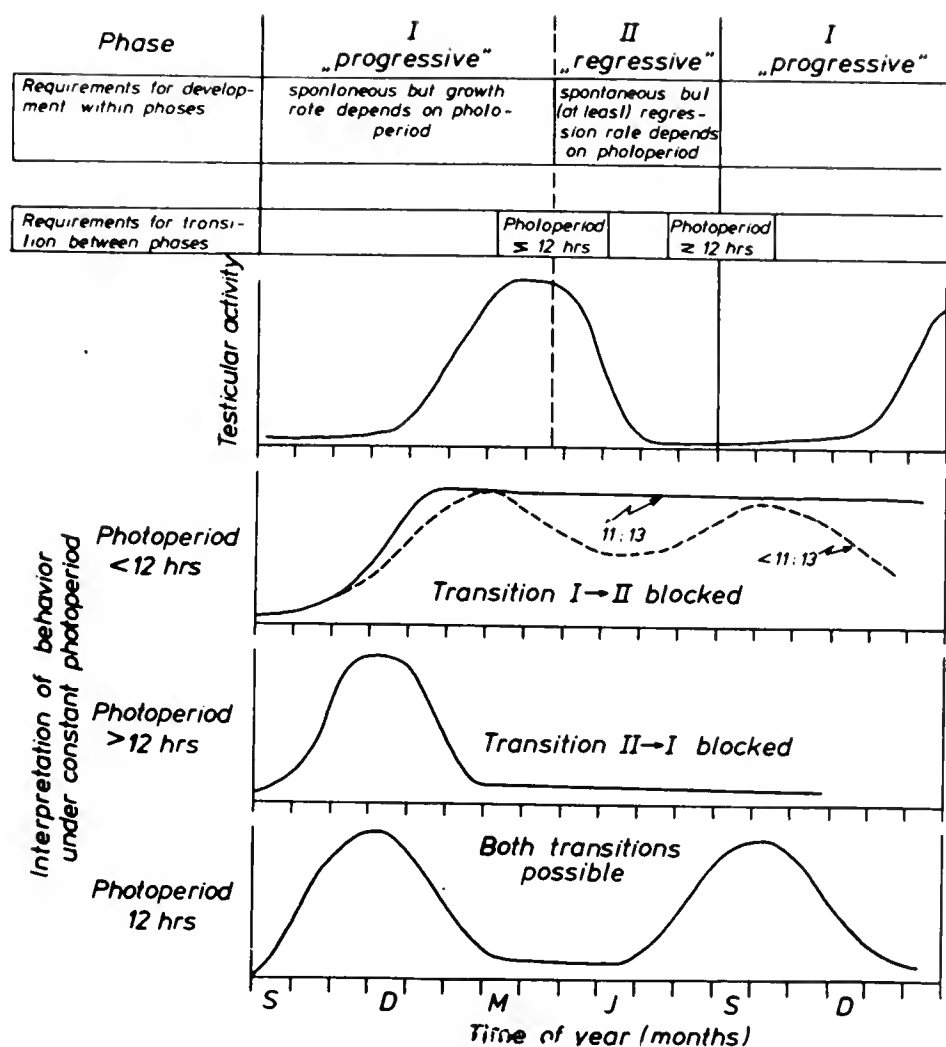


Fig. 9. Schematic representation of the annual reproductive cycle of the European starling and its endogenous and photoperiodic control. The dashed curve in the third diagram from below indicates that under some short photoperiods (e.g., a 6-h photoperiod; Schwab, Rudledge, 1975) variations in testicular size may occur which are different from the normal testicular cycle. For explanation see text

spontaneously is, however, drastically accelerated by long, and to a lesser degree also by very short, photoperiods. The effectiveness of these stimulatory photoperiods increases as time progresses.

Phase 2. For the transition to the next phase, the "regressive" phase, certain photoperiodic requirements are necessary. Details are not yet known but it appears that regression resulting in a state of photorefractoriness is possible under photoperiods longer than 11 hours, the rate of regression being partially dependant on photoperiod.

Photoperiods shorter than 11 hours also lead to a reduction in gonadal size but the situation is complicated here for two reasons: (1) Testicular regression occurred under short photoperiods in birds whose gonads had developed and sustained maximal size in an 11-h photoperiod (compare p. 511). Such regression, however, was only occasionally observed in birds whose testes had developed under the same short daylengths, i.e. an 11-h photoperiod (Fig. 4). Whether this indicates that the effectiveness of a short photoperiod to induce regression depends on previous photoperiodic history, remains to be elucidated. (2) There are qualitative differences in the kind of regression that occurs under photoperiods shorter or longer than 11 hours. Under shorter photoperiods the testes decrease in size but they often do not regress to the low values characteristic for birds whose testes regress under long day-

lengths. In addition, the beaks of the short-day birds usually remain yellow suggesting that testosterone is still being produced by the testes. Finally and most importantly, birds apparently do not become refractory when testes have regressed under short photoperiods (Burger, 1947, 1949; Falk, Gwinner, unpublished data).

If testes have involuted under long photoperiods, however, testicular growth does not occur in photoperiods of 12 hours or more. Only after the birds have been exposed to photoperiods of 12 hours or less for some time can the transition be made to phase 1 and testicular growth be initiated by long photoperiods.

Schwab (1971) and Rutledge and Schwab (1974) have shown that full testicular maturation can be induced during the photorefractory phase by exposing the birds to short days or even to constant darkness. We believe that these results can be incorporated in the present scheme by assuming that these short photoperiods first terminate photorefractoriness, thereby enabling the transition from phase 2 to phase 1 during which gonadal growth may then ensue.

On the basis of this scheme it becomes clear why the European starling develops a circannual rhythm in gonadal function under a 12-h photoperiod and only under a 12-h photoperiod. Within phases there appear to be spontaneous changes which may occur under many (phase 2) or all (phase 1) photoperiods, but the only photoperiod which allows both transitions to take place is the 12-h photoperiod. For the transition from the progressive phase (phase 1) to the regressive phase (phase 2) a 12-h photoperiod is just long enough to be effective. In contrast, for the transition from the regressive phase (phase 2) to the progressive phase (phase 1) the 12-h photoperiod is just short enough to be effective. Hence the circannual rhythmicity under the 12-h photoperiod owes its existence to the fact that transitions between both phases are possible in this photoperiod.

CONCLUSIONS

With regard to the limited ranges of permissive photoperiodic conditions, the circannual gonadal rhythm of the European starling provides perhaps the most extreme case among all circannual rhythms described so far. However, just because it provides such an extreme case it offers a unique opportunity for analyzing the factors, both external and internal, by which it is brought about. We are confident that a better understanding of the starling's circannual rhythm may subsequently help in the analysis of the apparently more complex circannual systems which have been described for other organisms.

ACKNOWLEDGEMENTS

This work was supported by the Deutsche Forschungsgemeinschaft SPP "Mechanismen biologischer Uhren".

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GONADOTROPIN RELEASE AND RHYTHMS OF CALLING BEHAVIOUR BY ENDOGENOUS OSCILLATOR IN QUAIL

Masaru Wada

Institute for Medical and Dental Engineering, Tokyo Medical and Dental
University, Kanda-Surugadai, Chiyoda-ku, Tokyo 101, Japan

Reproduction is closely related to time. It requires a timing for initiation of the processes to attain simultaneous maturity in the same species at the most favorable phase in a year. And reproductive processes themselves are time sequential events. Gonadotropin release in birds lived in Temperate Zone is induced by increasing day length. Then, gonadotropin in turn induces testicular growth and androgen secretion. These lead individuals to a mature stage ready for pair formation and consequent reproductive behaviors. So it is easy to speculate that the most, if not all, of the reproductive processes involve time measuring system to guarantee reproductive success. From a wide range of reproductive processes in Japanese quail, two aspects are chosen for examples how a time measuring system is deeply involved.

PHOTOSENSITIVE PHASE FOR LH SECRETION

In every experiment, Japanese quail (Coturnix coturnix japonica) were purchased from a commercial source at the age of 3 weeks and kept under non-photostimulatory short days upto 5 weeks before experiments were conducted. First, changes of circulating LH concentration after photostimulation were estimated (1). Samples were collected from the same birds by repetitive venipuncture after birds were transferred from 8L16D to 16L8D. LH was estimated by radioimmunoassay with modification for small samples. An LH rise from the base line concentration begins during the dark period following the first long day. This abrupt rise also occurs at the next dark period. This stepwise increase of LH concentration, at least during a first few days of photostimulation, indicates a circadian system underlying directly measures daylength. For daylength measurement, duration between 12 and 16 hour after dawn is important.

To detect exact phase in which light really means as a stimulatory information, light pulse of 30 min was given at the dark period of short days (Wada, 1979, 1981).

Quails were kept under short days of 8L16D, and the first blood collection was made around noon before treatment. During the following dark period, a photopulse was given at hour 18, 20, 22 and so on to each group, respectively. The second blood collection was made in the following morning. Changes of LH concentration were calculated from the initial and terminal values. The results indicates the existence of photosensitive or photoinducible phase for LH secretion in a day. Hamner (1964) has shown long before that finches measure photoperiodic time not with an hour glass but with a system involving circadian rhythms, conducting a so called resonance experiment. The photosensitive phase presents relatively limited duration in a day around 13 to 15 hours after dawn.

Is this rhythm of photosensitivity for LH secretion entrained to dawn or dusk? If the rhythm of the photosensitive phase starts at the daybreak,

the photosensitive phase for LH secretion still present at the same time whenever the light period of LD cycles are changed. But if the rhythm is entrained to dusk, photoinducible phase will advance when the light period is decreased and will delay when the light period is increased.

Whenever the light period of LD cycles is reduced from 8 hours to 4 hours or increased from 8 hours to 11 hours a peak is present at hour 22, that is 13 hours after dawn. No apparent shift occurred (Hamner, 1964).

The rhythm of photosensitivity for LH secretion is circadian. It freeruns under constant darkness in White crowned Sparrow. To get a clue from another side, a Nembutal injection experiment was conducted (Follett et al., 1974). Barbiturate injection before the critical period on the day of proestrus in female cycling rats was shown to cause a 24 hour delay in ovulation (Everrett, 1964; Everett, Sawyer, 1950) and in preovulatory LH release (Stetson, 1977).

A photoperiodic schedule was 8L16D plus 30 min photopulse at hour 22, 13 hours after dawn. The first blood collection was made in the morning before treatment, and the second collection was made in the following morning. During the dark period in which period a photopulse was delivered, a single shot of pentobarbital (5 mg/100 g BW) was given at various time to groups of birds, respectively. At several points, saline was injected as controls. Changes in LH concentrations was calculated from initial and terminal values.

Only when the injection of Nembutal was given at hour 22, apparent cancellation of LH release was observed. Saline injection did not cause LH release practically. This results seems to indicate several things. Since the effective duration of Nembutal is upto 1 hour and injection is single, this cancellation of LH release is due to blockade of photic information transfer to the neuroendocrine machinery. If it acts on the oscillatory mechanism, injection before this time may cause disturbance of photosensitive phase, resulting cancellation of LH increase by photopulse. And if Nembutal acts on LH RH and the adenohipophysis axis, injection after this time may cause blockade of LH secretion. It may indicate that transfer of photic information is processed in a short time and that lag time between photostimulation and induction of LH release is due to delay of the neuroendocrine processing.

RHYTHMS IN CALLING AND LOCOMOTOR ACTIVITY

What I have mentioned is how quail detect timing for initiation of physiological changes. For a good chance of reproductive success, however, interindividual communication is also necessary for the next step. Androgens have a key role for this.

Japanese quail show a characteristic crow at sexual maturity. Enough evidences are still lacking for its ecological roles (Cariou, 1969; Potasch, 1974) it seems to be involved in pair formation. Since it is easier to record calling continuously, I chose this calling for a quantitative study of behavior together with locomotor activity.

Experimental birds were placed in a recording cage. The floor of the recording cage moves as a seesaw, and each deflection of the floor triggers an installed microswitch. The cage was placed in a chamber which is light tight and ventilated through a light tight trap by a motor driven fan. Inside the box illumination was provided by an overhead fluorescent lamp

through frosted glass. To prevent sudden changes of temperature when light signals are given, the lamp is covered by a water jacket with continuous water flow. A small microphone is placed to pick up a crow, which connected to an electronic device composed of a bandpass filter, a comparator and a timer. With this device, one crow is converted into a pulse. This pulse by a calling and floor deflection by locomotion are counted and printed out every clock hour (Wada, 1981).

The mean numbers of calling and locomotor activity in a group of 5 intact quails indicated that they began to call several hours before lights are turned on and a very sharp peak was present at the first one hour after light on. There were also increases and decreases in locomotor activity. Castration completely abolished calling and reduced locomotor activity very much. And Silastic implants containing crystalline testosterone recover numbers of calling and locomotor activity to the precastration level. Moreover, patterns of calling reappear, even though testosterone is released from the implanted capsules steadily (Wada, 1981).

Is this sharp peak mere a response to a light on? Or this pattern means that calling is circadian. Anticipatory calling before light seems to indicate that the latter idea is correct. To test this possibility, I conducted an experiment whether calling freeruns or not (Wada, in prep.).

Instead of normal LD cycles, light and dim light (200 and 0.1 lux) cycles were made and castrated and implanted quail were kept under these condition. Quail also showed a rhythmic pattern of calling, a peak of which advanced a little in this condition. Calling clearly freeruns under constant dim light. Locomotor activity also freeruns with almost the same tau to calling. This clearly shows that calling and locomotor activity is circadian. Auto-correlation of both behavior and cross-correlation between two behaviors under constant dim light were calculated. The results showed significant auto-correlation in both calling and locomotor activity. Also cross-correlation between two behaviors is significant with fixed phase relationship of 3 hours.

It may be too much to say that the circadian oscillatory mechanism involved in driving photosensitivity for LH secretion and that drives sexual behaviors are the same. However, in reproduction in male birds this system is deeply involved and that allows them successful production of their offsprings.

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Symposium

ADAPTATION OF BIRDS TO HIGH LATITUDES AND MOUNTAINS

Convener: F. SALOMONSEN, DENMARK

Co-convener: A. ANDREEV, USSR

PARMELEE D.F.

POLAR ADAPTATIONS IN THE SOUTH POLAR SKUA (CATHARACTA MACCOR-MICKI) AND THE BROWN SKUA (CATHARACTA LONNBERGI) OF ANVERS ISLAND, ANTARCTICA

JOHNSON ST.R.

ADAPTATIONS OF THE LONG-TAILED DUCK (CLANGULA HYEMALIS) DURING THE PERIOD OF MOLT IN ARCTIC ALASKA

MELTOFTE H.

POPULATIONS AND BREEDING SCHEDULE OF WADERS IN HIGH ARCTIC GREENLAND

SALOMONSEN F.

ALTITUDINAL ADAPTATION IN BODY PROPORTIONS OF BIRDS

BROWN R.G.B.

THE INFLUENCE OF ICE ON THE ECOLOGY OF ARCTIC AND ANTARCTIC SEABIRDS

KOVSHAR A.F.

POLYCYCLICITY AND HYPOMORPHIC EFFECT IN REPRODUCTION OF MOUNTAIN BIRDS

KRETCHMAR A.V., SYROETCHKOVSKY E.V.

ECOLOGICAL ADAPTATIONS OF THE SNOW GOOSE (ANSER CAERULESCENS) TO HIGH-LATITUDE ENVIRONMENT

POLAR ADAPTATIONS IN THE SOUTH POLAR SKUA (CATHARACTA MACCORMICKI)
AND THE BROWN SKUA (CATHARACTA LONNBERGI) OF ANVERS ISLAND, ANTARCTICA

David F. Parmelee

Field Biology Program, 349 Bell Museum, University of Minnesota,
Minneapolis, Minnesota 55455, USA

INTRODUCTION

Ornithologists in recent years have become increasingly interested in the ecology and behavior of southern skuas, notably the widely accepted monotypic South Polar Skua (Catharacta maccormicki) and the much debated Brown Skua (C.lonnbergi)¹ which appears to be polytypic with uncertain evolutionary affinities. Although a number of workers have observed either one or the other in various parts of the Antarctic and Subantarctic, few have had the opportunity to make comparative studies. However, since 1963 Young (1963a, 1963b, 1970, 1972, 1977, 1978) has reported on each respectively in the vastly separated breeding grounds adjacent to the Ross Sea and on islands near New Zealand.

Most of the known breeding grounds of these two skuas are separated. A narrow zone of overlap exists in the South Shetlands and Antarctic Peninsula areas between 62° and 65°S, and recently South Polar Skuas bred on the South Orkneys where only Brown Skuas were known to breed previously. Where these skuas occur sympatrically, they often breed within sight of one another and occasionally hybridize. Trivelpiece et al. (1980, 1982) reported on the mixed breeding grounds of Point Thomas, King George Island, South Shetlands, where nesting Brown Skuas outnumber nesting South Polar Skuas by slightly more than two to one.

Since 1974, Parmelee et al. (1975, 1977, 1978, 1979), Parmelee (1980), and Pietz et al. (1980) reported on the mixed breeding grounds of Anvers Island near the Antarctic Peninsula where, conversely, nesting South Polar Skuas at times outnumber nesting Brown Skuas by 100 to one. The purpose of this report is to show how the two skuas adapt to polar life on Anvers Island where in certain areas they reside next to one another under identical environmental conditions.

Skua observations began at Palmer during the 1973-1974 austral season; intense study of them was carried on by D.R.Neilson from 1974-1975 through 1977-1978, and by P.Pietz from 1979-1980 through 1980-1981. The study ended with the 1980-1981 season.

STUDY AREAS AND METHODS

The study centered at U.S. Palmer Station (64°46'S. 64°03'W) on the south coast of Anvers Island. The study area (Figure 1) included the station and several moss- and lichen-covered rocky peninsulas and off-shore islets that are mostly free of snow in summer. The rest of Anvers Island is covered with a perpetual ice sheet that rises abruptly behind the station.

¹ Subantarctic Skua (Catharacta antarctica madagascariensis) is the appropriate synonym for Brown Skua (C.lonnbergi), according to Brooke (1978).

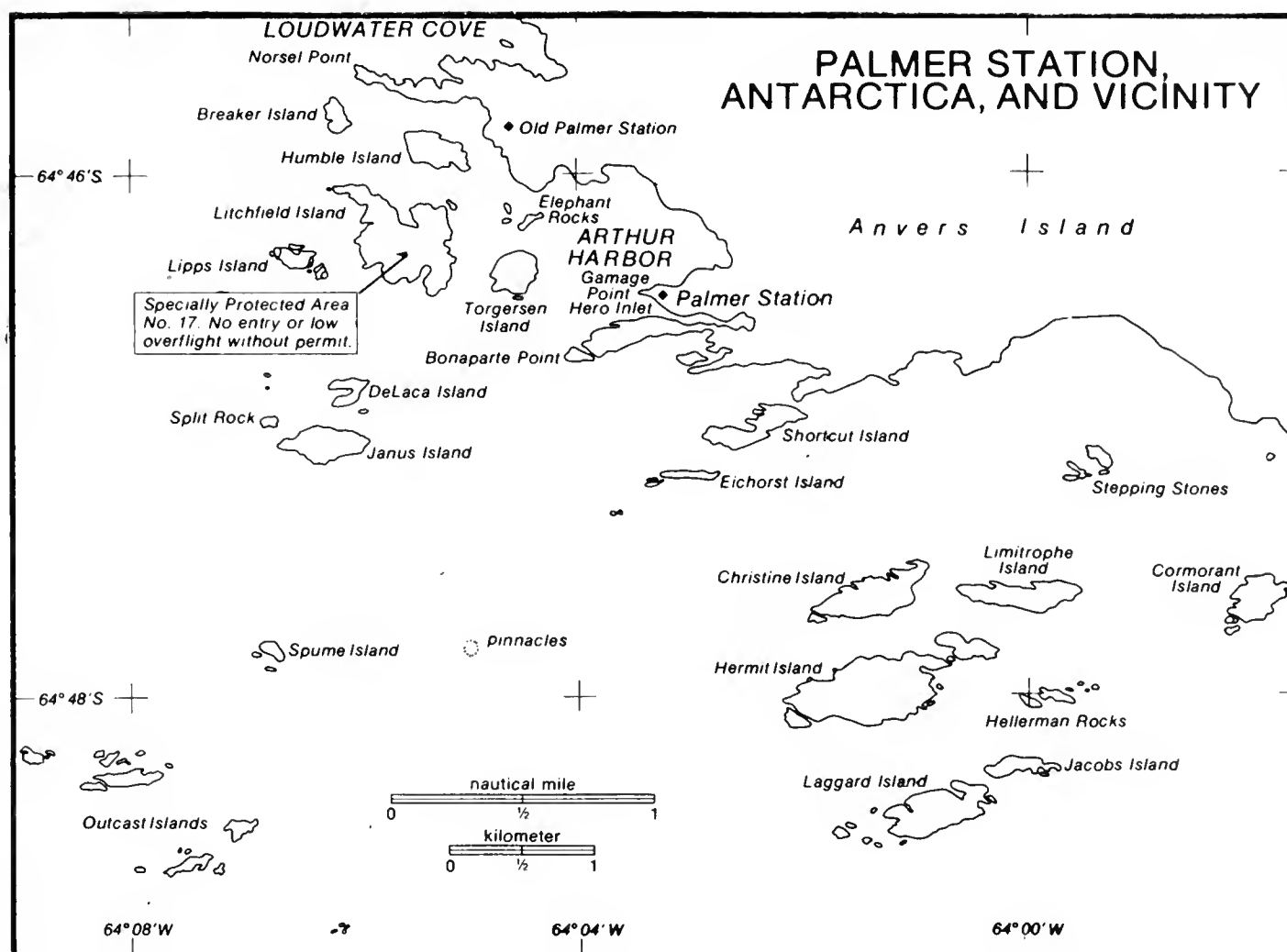


Fig. 1. Palmer Station study area, Anvers Island, Antarctica

While the overall climatic milieu of Anvers Island changes little from year to year, the temporal extent of the surrounding oceanic pack ice can vary dramatically within and between seasons. Although the summer pack is usually less extensive than winter ice, strong winds at times concentrate it against the shores for extended periods, forcing all surface-feeding birds to fly long distances from their breeding spots to open sea areas. Probably more than any other physical factor, the position of the pack ice cover in summer influences their feeding, and consequently their breeding success (Parmelee et al., 1978).

Rubber boats (zodiacs) powered by outboard engines provided access to the outlying skua breeding grounds, except Bonaparte Point which could be reached any time by means of a hand-operated cable trolley. Adult skuas were captured by hand nets while they defended their nests and by large cannon nets at areas baited with food scraps. Captured skuas were banded with lock on aluminum bands and later with tough Swedish-made metal rings engraved with numbers provided by the U S Bird Banding Laboratory. In addition many were banded with colored metal or plastic rings for coding purposes and convenient field identification of individuals.

DEPARTURES-MIGRATIONS-ARRIVALS

Winter-over observations of Neilson in 1975, W.R.Fraser in 1976, R.Glass in 1977 and N.Bernstein in 1979 document the departure of both South Polar and Brown Skuas from the Palmer area for the austral winter. Following the fledging of chicks, which commences in mid-February and continues into March, numbers of young and adults drop perceptibly by mid-April. Few skuas are seen in May. The latest observation for a South Polar Skua of any age is 25 May (one bird), for a Brown Skua, 2 May (one bird). Holdgate (1963)

T a b l e 1. Long-distance banding recovery data for South Polar Skuas banded prior to fledging near Palmer Station, Anvers Island

| Band Number | Date Banded | Date Recovered | Recovery Locality |
|-------------|------------------|-------------------|-----------------------------|
| 877-34210 | 16 January 1975 | 14 September 1975 | Sonora, Gulf of Mexico |
| 877-34271 | 20 January 1975 | 31 July 1975 | Godthabsf Jorden, Greenland |
| 877-36534 | 14 January 1976 | 18 December 1976 | Paco Do Luminar, Brazil |
| 877-36556* | 18 January 1976 | 23 May 1980 | 42 SE Paranagua, Brazil |
| 877-36580 | 12 February 1976 | Winter 1976 | Iati, Brazil |
| 877-36900 | 10 January 1977 | 10 January 1978 | ILHA Santana, Brazil |
| 877-36723 | 23 February 1977 | 30 October 1980 | N R Macou Coast, Brazil |
| 1057-10116 | 11 February 1979 | 27 June 1979 | Recife, Brazil |
| 1057-10377 | 22 February 1980 | 9 July 1980 | Bullards Beach, Oregon |

* South Polar Skua x Brown Skua hybrid.

observed similar departure times for Palmer during 1955-1957, though he did not distinguish between the two species. We have no Palmer records of skuas for June, July, August, or September, although other birds often are observed during this period.

According to Neilson (unpublished thesis), fledging South Polar Skuas are the first of their species to leave the Palmer area, soon followed by the breeding females; breeding males linger at the nesting spots for a number of days before departing. South Polar Skuas from the Palmer area fly northward across the Drake Passage and continue along the Atlantic and Pacific Coasts of South America. Some of them enter the Northern Hemisphere and follow the coasts of Central and North America, at least as far north as the State of Oregon on the Pacific and West Greenland on the Atlantic. From aboard ship we have seen migrating skuas over the Drake Passage. Upon reaching South America they do not, however, always remain close to land, for we have sighted them far out at sea some 320 kilometers east of Argentina. Nine Palmer-banded skua chicks have been recovered to date (see Table 1).

According to Table 1, it is clear that some juvenile South Polar Skuas migrate long distances in a short time, as exemplified by the July recovery in Greenland (see Salomonsen, 1976) following a probable April departure from Palmer. Furness (1978a) concludes that Great Skua (C.skua) juveniles and older prebreeders migrate considerable distances in the Northern Hemisphere, but their winter movements become much shorter when they are more than five years old. Since we do not have long-distance recoveries of Palmer-banded adults, we can only speculate on their winter movements. We have no long-distance recoveries for Brown Skuas of any age. Furness also concludes that the Great Skua in its first year suffers high mortality. Seven of the nine Palmer-banded chicks were first-year birds when recovered.

Both species return to Palmer in October, our earliest date for South Polar Skuas being 13 October (both sexes), and 25 October for Brown Skuas (sexes uncertain). Holdgate (1963) first recorded skuas (species uncertain) each year during 1955-1957, from 19 to 23 October. From the time of first

arrival, the numbers of South Polar Skuas increase daily until by mid-November the birds are conspicuous in many nesting and non-nesting areas. By mid-November the much less abundant Brown Skuas are mostly settled on their nesting spots in a few select areas close to penguin colonies.

FEEDING STRATEGIES

Feeding skuas are opportunists personified. Much has been written about their diets and feeding habits, e.g. Furness et al. (1981a, 1981b), as well as their predation techniques, e.g. Furness (1978b), Sinclair (1980), Maxson et al. (in press). Although the feeding strategies of breeding South Polar and Brown Skuas may be similar where the two breed allopatrically, they may be strikingly different on sympatric breeding grounds. For example, Neilson soon found that where the two co-exist on Anvers Island, the South Polar Skuas as a rule fly out to sea for considerable distances to obtain fish and krill for their young whereas the Brown Skuas get most of their food requirements close by from the eggs and chicks of Adelie Penguins (Pygoscelis adeliae). In sharp contrast, I found South Polar Skuas nesting adjacent to and feeding their chicks on penguins in an area unoccupied by Brown Skuas on the west coast of Anvers Island less than 30 kilometers from our Palmer study area.

At Palmer the numbers of breeding South Polar Skuas fluctuate from one year to the next, at times dramatically. For example, during the 1979-1980 season, Pietz (pers. comm.) estimated approximately 300 nesting pairs in the study area, in 1980-1981, over 550 pairs. The birds nest most anywhere on exposed ground from near the beaches to high ridges inland. The small numbers of Brown Skuas are stable by comparison.

To date there is considerable evidence that the breeding schedules of skuas relate to the availability of prey species (see Stonehouse, 1956; Young, 1977; Trivelpiece et al., 1982). If this hypothesis is valid, we have a partial explanation why skuas of the same species often show highly asynchronous breeding schedules even when confined to a single, isolated island. The best example of this kind of behavior that I have observed took place on Marion Island in the Indian Ocean: a pair of Brown Skuas that had established itself at a colony of early-nesting Blue Petrels (Halobaena caerulea) actually produced chicks before any eggs had been laid by neighboring Brown Skuas that were dependent upon latenesting penguins and prions.

In preventing the artificial feeding of birds at Palmer Station, we closed the open dumps and prohibited hand feeding of individuals. The one exception was a pair of color-banded South Polar Skuas that had become station pets. They nested each year on Bonaparte Point and regularly flew across ice or open water to the station to be fed. Although some South Polar Skuas nested as early or earlier than this pair during favorable years, the station pets produced a chick long before any of the others during those seasons when unfavorable ice conditions resulted in many late and often aborted nestings. And, unlike the others, the pets fiercely defended a feeding territory (station balcony), and thus their behavior was like that of Brown Skuas that defended feeding territories when residing next to penguin rookeries. Trivelpiece et al. (1982) had similar experiences with a pair of South Polar Skuas that nested early after adapting to an artificial food supply.

Neilson believed that the asynchrony exhibited by the South Polar Skuas in the Palmer study area is probably due to the availability of fish and krill over the entire breeding season. The birds simply are not under pressure to adjust their schedules to that of their prey in the sense that the Brown Skuas are with respect to penguins.

No doubt other factors besides prey availability contribute to the asynchronous laying schedules of skuas. Not all skuas arrive at the same time, and the late arrivals simply pair and lay later. Presumably the older, well established birds breed earlier on the average than the younger, inexperienced ones, but we lack hard data for the skuas in this respect.

EGG LAYING SCHEDULE

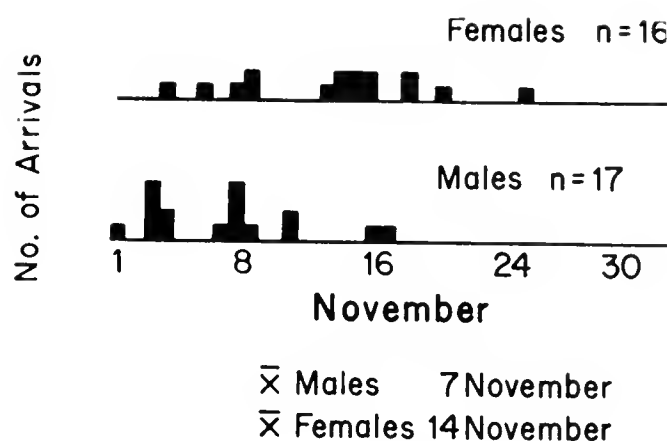
A most critical time in the breeding cycle of the two skuas is the clutch initiation date. By the time eggs appear we assume that the female has responded favorably to various stimuli such as male attentiveness, food supply, nest site conditions, etc. We also assume that if the two skuas breeding sympatrically lay at different times, the chance for cross mating will be diminished, since asynchronous egg laying conceivably is an important mechanism for maintaining the integrity of species. Watson (1975) and Trivelpiece et al. (1980) report that the clutch initiation date is significantly earlier in Brown Skuas than in South Polar Skuas. Trivelpiece et al. (1980) also found significant differences in breeding times between those Brown Skuas occupying optimal feeding territories and those with suboptimal ones; he also noted that the hybridizing pairs followed a South Polar Skua breeding schedule.

Our initial observations at Palmer (Parmelee et al., 1977) showed little if any asynchrony in egg laying between the two skuas. Trivelpiece et al. (1980) believed that this unexpected observation related directly to late breeding in the penguins: Since penguins lay later at Palmer than at King George Island, it follows that the Brown Skuas of Palmer also lay later—about the time that the South Polar and hybridizing pairs lay. We find Trivelpiece's reasoning valid but only with modification.

Further analysis of data from several seasons at Palmer suggests that the Brown Skuas lay significantly earlier than do the South Polar Skuas (Neilson, unpubl. dissertation and Pietz, pers. comm.). When pack ice conditions at Palmer are favorable, assuming that an early food supply is abundant as well as accessible, it is true that some South Polar Skuas commence breeding as early as the Brown Skuas. When pack ice conditions are not favorable, however the onset of egg laying in the South Polar Skuas can be much delayed and even aborted some years. During seven consecutive breeding seasons at Palmer, only three proved highly favorable for the surface-feeding South Polar Skuas. The penguin-dependent Brown Skuas had six very successful seasons during this same period, losing one not to ice conditions but rather to a fowl-cholera outbreak to which they were particularly susceptible (Parmelee et al., 1979).

Most Brown Skua nesting sites are occupied by pairs early in the season. Many South Polar Skua sites, are, however, occupied only by males for several days, suggesting that the majority of males arrive well in advance of their mates. This is precisely what Neilson found when he overwintered at Palmer and observed the arrival of a good sample of his color-marked birds of both

Fig. 2. 1975 spring arrival dates of marked South Polar Skuas breeding on Bonaparte Point, Anvers Island. From Neilson (unpublished dissertation)



sexes. At 17 nest sites on Bonaparte Point, mapped during January–February 1974 when the birds were identified to sex, he recorded the return arrivals of 17 males and 16 females at these same sites the following November. According to Neilson, the males arrived significantly earlier ($t = 19.868$, $p < 0.001$) than the females (Figure 2); in no case did the female member of the pair arrive earlier than her mate.

From these data we conclude that although a few South Polar Skua females may be among the earliest returning to the Palmer breeding ground, a female majority probably arrives after a male majority has already settled on the nesting sites. There can be little question that a male South Polar Skua advertising for a mate is a powerful inducement for a reproductively primed female Brown Skua bent on finding a mate on a breeding ground where all available Brown Skua males are paired. Unattached Brown Skuas will at times even displace the female of an established pair of South Polar Skuas. Pietz (pers. comm.) noted that one South Polar Skua female was displaced and probably killed by a Brown Skua that later paired with the luckless bird's mate in the formation of a hybrid bond.

It is no accident that all known hybrid pairs at Palmer and King George Island consist of male South Polar Skuas x female Brown Skuas. Once the hybrid bond forms, a certain degree of mate fidelity exists in successive years as shown in Table 2.

Generally, the male South Polar Skuas of mixed pairs forage at sea and return to the nest site mostly with fish and krill. During those years when ice conditions prevent successful foraging, nesting attempts and even pair formation may be aborted. This was most evident to Neilson during the ice-bound season of 1977–1978 when only seven pairs of South Polar Skuas attempted to nest and produced no chicks, compared to the previous season when 261 pairs produced many chicks in the same area. As expected, no mixed pairs formed during the 1977–1978 season, clearly indicating that certain physical factors such as adverse ice conditions also inhibit crossmating. The ice prevents proper feeding and thus stymies courtship feeding by the male and receptiveness by the female.

As a rule the nesting areas of mixed pairs did not include feeding territories and thus were typical of South Polar Skua sites. The one exception was a pair that bred consecutively for three seasons on Cormorant Island. Their defended ground included both nesting site and an adjacent penguin colony from which the female obtained food. Otherwise, we were unable to track the female Brown Skua of mixed pairs closely, for the bird invariably flew from view. The female of a mixed pair under surveillance by Pietz (pers.

Table 2
Mixed pairs (♂ South Polar Skua x ♀ Brown Skua) recorded in Palmer Study Area during breeding seasons 1974-1975 through 1980-1981. The 14 cross matings produced 27 eggs and 24 hybrid young, 17 of which fledged. From Neilson (unpublished thesis) and Pietz (personal communication)

| | | 1974 - 1975 | | 1975 - 1976 | | 1976 - 1977 | | 1977 - 1978 | | 1978 - 1979 | | 1979 - 1980 | | 1980 - 1981 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
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| Mixed Pair | Identity | Locality | | Eggs | Young | Fledged | Eggs | Young | Fledged | Eggs | Young | Fledged | Eggs | Young | Fledged | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | S.P. ♂ 977-31504 x Brown ♀ 877-36911 | Humble | | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | ♂ 977-31504 no return ♀ 877-36911 mated with Brown ♂ | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | S.P. ♂ 877-36957 x Brown ♀ 877-36958 | Humble | | | | | 2 | 2 | 2 | 2 | 2 | 1 | 0 | ♂ 877-36957 no remate ♀ 877-36958 mated with Brown ♂ | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 3 | S.P. ♂ 877-36964 x Brown ♀ 977-31562 | Hermit | | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 0 | ♂ 877-36964 mated with S.P. ♀ ♀ 977-31562 no return | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 4 | S.P. ♂ 877-34049 x Brown ♀ 877-34048 | Cormorant | | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | Paired but produced no eggs | ♀ 877-34048 paired with unbanded Brown ♀ but did not nest | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 5 | S.P. ♂ unbanded x Brown ♀ color banded | Shortcut | | | | | 1 | 1 | 1 | No return | | | | No return | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 6 | S.P. ♂ 877-36953 x Brown ♀ 877-36908 | Humble | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | </ |

comm.) on Humble Island clearly avoided nearby penguin feeding territories that were vigorously defended by Brown Skua pairs. Instead she flew out of sight, presumably to undefended areas for food, returning with penguin remains: On one occasion she foraged for fairy shrimp in a freshwater pond. According to Pietz, the penguin diet of at least one pair of Brown Skuas was supplemented by krill in February and by fish after the young penguins had fledged.

To date we do not know whether the hybrid young are fertile. Sexual maturity comes late in skuas, and none of our marked birds have been found nesting so far. So few marked young from the many pure pairs have been noted in the study area that we cannot help but speculate on their whereabouts, especially of birds four years or older. It is also apparent to us that hundreds of unbanded pre-breeders keep showing up in the study area year after year, clearly indicating that skuas move about a great deal. Where these prebreeders come from we have no idea. In this we are reminded of Brooke (1978) who cautions against collecting non-breeding specimens for taxonomic purposes, for who knows how many forms of skuas are among the wide ranging pre-breeders.

With so many pre-breeders on a breeding ground, not to mention late-nesting pairs, one is inclined to think of some of these birds as floaters - individuals capable of breeding but unable to find mates or nesting areas. Brown Skuas especially are pressured to find good spots near penguins. Earlier Parmelee et al. (1979) reported a heavy mortality of nesting Brown Skuas as a result of a severe fowl cholera epidemic at Palmer in 1978-1979. The following season we expected to find all the vacancies filled by new birds, but did not. Most of the vacated territories remained undefended throughout the breeding season; they were not even taken over by the abundant and opportunistic South Polar Skuas close by. We have no explanation for this unexpected event, except that it gives credibility to the belief that rigidly maintained skua territories of long standing retain their stability for a period following a vacancy (Young, 1972). However, by 1980-1981 many of these vacated territories were used again.

DISCUSSION

The evolutionary history of the world's skuas (Stercorariidae or Stercorariinae) has been debated for years. More recently Devillers (1978), while recognizing the genus Stercorarius for both the large skuas and small skuas (jaegers), concluded that the large ones consist of three species: the monotypic South Polar or McCormick's Skua (S.maccormicki), the monotypic Chilean Skua (S.chilensis), and the polytypic Northern or Great Skua (S.skua) which is made up of four allopatric races - S.s.skua, the nominate race; S. s. antarcticus, the Falkland Skua; S. s. lonnbergi, the Brown Skua and S. s. hamiltoni, the Tristan da Cunha Skua. Devillers believes that the North Atlantic was "almost certainly colonized" from Tristan da Cunha or the Falklands, since these islands have the most "skua-like" birds of any southern population, are closest geographically, and directly linked to the northern breeding grounds by migrating procellariid seabirds that are often accompanied by skuas.

On the basis of differences in juvenile plumages, Brooke (1978) supports the widely recognized genus Catharacta for the large skuas while maintaining

Stercorarius for the small ones. He agrees with Devillers in that the South Polar and Chilean Skuas are monotypic, but for lack of hard evidence sees no clear connection between any of the southern skuas and the Northern Skua skua which he considers monotypic. He also states that the South Polar Skua is the one that could most easily establish a northern offshoot because of its extensive northward migrations. Following an exhaustive review on nomenclature priorities, including a re-examination of type specimens, Brooke concluded that the remaining southern skuas are conspecific and should be classified as follows: nominate Catharacta antarctica antarctica of the Falklands and Patagonia, C.a.hamiltoni of the Tristan da Cunha group, and the widely distributed C.a.madagascariensis which replaces the name lonnbergi, except perhaps in the New Zealand area where some evidence exists for a distinct race based on nuptial plumage characteristics.

Generally, we favor the Brooke hypothesis, but since we do not wish to muddy the taxonomic waters of the skuas further with additional speculation and changes in nomenclature at this time, our views on skua taxonomy are confined to the South Polar and Brown Skuas and based primarily on evidence from our studies on Anvers Island. Even though the two skuas hybridize in zones of overlap, we believe that they should be classified as distinct species, as usually is the case at present.

We envision our Palmer study area to be fairly typical of Short's (1969) description of a zone of overlap and hybridization where secondary intergradation has occurred. Palmer has two taxonomically significant features: (1) the presence of numerous parental phenotypes that are morphologically distinct and show partial reproductive isolation; (2) its parental phenotypes are sympatric and include primary (F1) hybridization, competition, and reinforcement of isolating mechanisms. At Palmer we have shown that even though conditions arise which result in crossmatings of a few individuals, also evident are certain mechanisms for keeping the two species apart, notably different food, feeding, and territorial strategies, and asynchronous breeding times. No hybrid swarms have been noted as well. According to Short (1969), factors such as these suggest impediments to gene flow.

Whether the hybrids prove fertile or not, we prefer to think of the parental forms as semispecies which, according to Short (1969), are one type of allospecies comprising a superspecies and, therefore, taxonomically they are species. The concept has appeal, for our Palmer skuas clearly show a very close though separate relationship.

SUMMARY

South Polar and Brown Skuas were studied under identical environmental conditions near Palmer Station, Anvers Island, Antarctica during seven breeding seasons from 1974 to 1981. Their departures, long-distance migrations and arrivals are described. Feeding and territorial strategies differ greatly where the two species breed sympatrically, but not necessarily differing where they breed allopatrically. Surface-feeding South Polar Skuas are sensitive to pack ice conditions and other climatic conditions affecting foraging, whereas the penguin-dependent Brown Skuas are not. Brown Skuas appear to be particularly susceptible to outbreaks of fowl cholera, and their va-

cated territories are not quickly filled. Parental phenotypes of both skuas are distinct and common on Anvers Island, hybrids comparatively rare. Conditions favoring and also inhibiting cross matings, are discussed, as are the mechanisms for partial reproductive isolating systems. The two skuas at Palmer are considered semispecies in a zone of overlap and hybridization and classified as separate species.

ACKNOWLEDGMENTS

This study was supported by National Science Foundation grants OPP74-21374, DPP76-15350, and DPP77-22096. G.Jonkel of the U S Bird Banding laboratory provided banding assistance. N.P.Bernstein, W.R.Fraser, B.Glass, S.J. and G.D.Maxson provided field assistance. Special thanks to D.R.Neilson and P.J.Pietz for use of their field data and help with the manuscript.

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ADAPTATIONS OF THE LONG-TAILED DUCK (CLANGULA HYEMALIS L.)
DURING THE PERIOD OF MOLT IN ARCTIC ALASKA

Stephen R. Johnson

LGL Alaska Research Associates, Inc., Fairbanks, AK,
99708 and LGL Ltd., 10110-124 Street, Edmonton, Alberta, Canada

INTRODUCTION

The Long-tailed Duck, or Oldsquaw (Clangula hyemalis L.) is probably the most numerous and the most widely distributed duck in the Arctic and Subarctic (AOU, 1957; Vaurie, 1965; Bellrose, 1976; Palmer, 1976; Cramp, Simmons, 1977). The total North American population has been conservatively estimated to be 3 to 4 million birds (Bellrose, 1976). Considering the expanse of tundra nesting habitat occupied by this species in other parts of the hemisphere, e.g., Northern Europe and Siberia, a reasonable estimate of the size of the worldwide population may be in the order of ten million (10^7) birds.

At least 250 000 and possibly as many as one million Long-tailed Ducks migrate into the Beaufort Sea area each May and June. Although most follow coastal and offshore migration routes, a large number also fly through interior Alaska and over the Brooks Range to reach the north coast (Richardson, Johnson, 1981).

In late June and early July, post-breeding male seaducks abandon the incubating females and begin to move toward communal molting areas on lakes or in coastal areas. Molting areas used by males may be near the breeding areas, but frequently are hundreds or even thousands of km away (Salomonsen, 1968). Along the north coast of Alaska, tens of thousands of male Long-tailed Ducks congregate in coastal lagoons during the molt period in mid-July to mid-August; many probably have traveled relatively short distances from adjacent tundra breeding areas. The males are incapable of flight for several weeks during this period as they shed and regrow their flight feathers. This paper discusses several important adaptations of male Long-tailed Ducks during their molt in Arctic Coastal Alaska.

STUDY AREA

Detailed descriptions of the 1974, 1975 and 1977-1981 study areas in Northern Alaska and the Yukon Territory (Y.T.) appear in Johnson et al. (1975) and Johnson and Richardson (1981). In general, the Arctic Coastal Plain (Wahrhaftig, 1965) is an area of low arctic tundra bordered by the Brooks Range on the south and the Beaufort Sea on the north (Fig. 1). The Plain is narrow (± 20 km) along the Yukon north coast (Salter et al., 1980) and widens (± 150 km) toward the west. Most of the research reported here has been conducted along the fringe of the Arctic Coastal Plain between Oliktok Point, Alaska, and Herschel Island, Y.T. Most of the Coastal Plain is bordered by a chain of tundra- or gravel-covered barrier islands, many of which are 3-7 km offshore. The intervening areas, between the coastal plain and the barrier islands, are brackish lagoons and embayments 2-5 m deep.

The most intensive investigations of C.hyemalis have been conducted in the Simpson Lagoon area of Alaska (Fig.1, inset). A detailed description of this area is given in Johnson and Richardson (1981).

CLIMATE

The Climate of the Arctic Coastal Plain is Polar Continental (Brower et al., 1977) and is characterized by long cold winters and short cool summers; frost and snow can occur on any day of the year. Most of the precipitation falls as rain during the months of July and August and there is considerable seasonal variation from year to year. Timing of snow and ice melt (Benson et al., 1975; Holmgren et al., 1975) greatly influences the availability of habitat to birds. Snow melt begins in late May and is usually complete in exposed areas by mid-June. Deltas of rivers provide the first available habitat for waterfowl and other waterbirds. Most lakes and ponds are icefree by late June. Most of the shallow coastal lagoons are frozen to the bottom until early June when decomposition of the lagoon ice is accelerated by the flood of relatively warm river runoff. The lagoons are generally ice-free by early July.

Polar pack ice covers the Beaufort Sea for 8-9 mo of the year although cracks, leads and polynyas may be present off shore throughout the winter. Cracks and holes in the sea ice north of the barrier islands begin to open by mid-July. Storms with northeast winds and high waves occur irregularly during July-September; severe storms from the west or southwest occur most often during August-October and may blow floating ice back toward shore.

METHODS

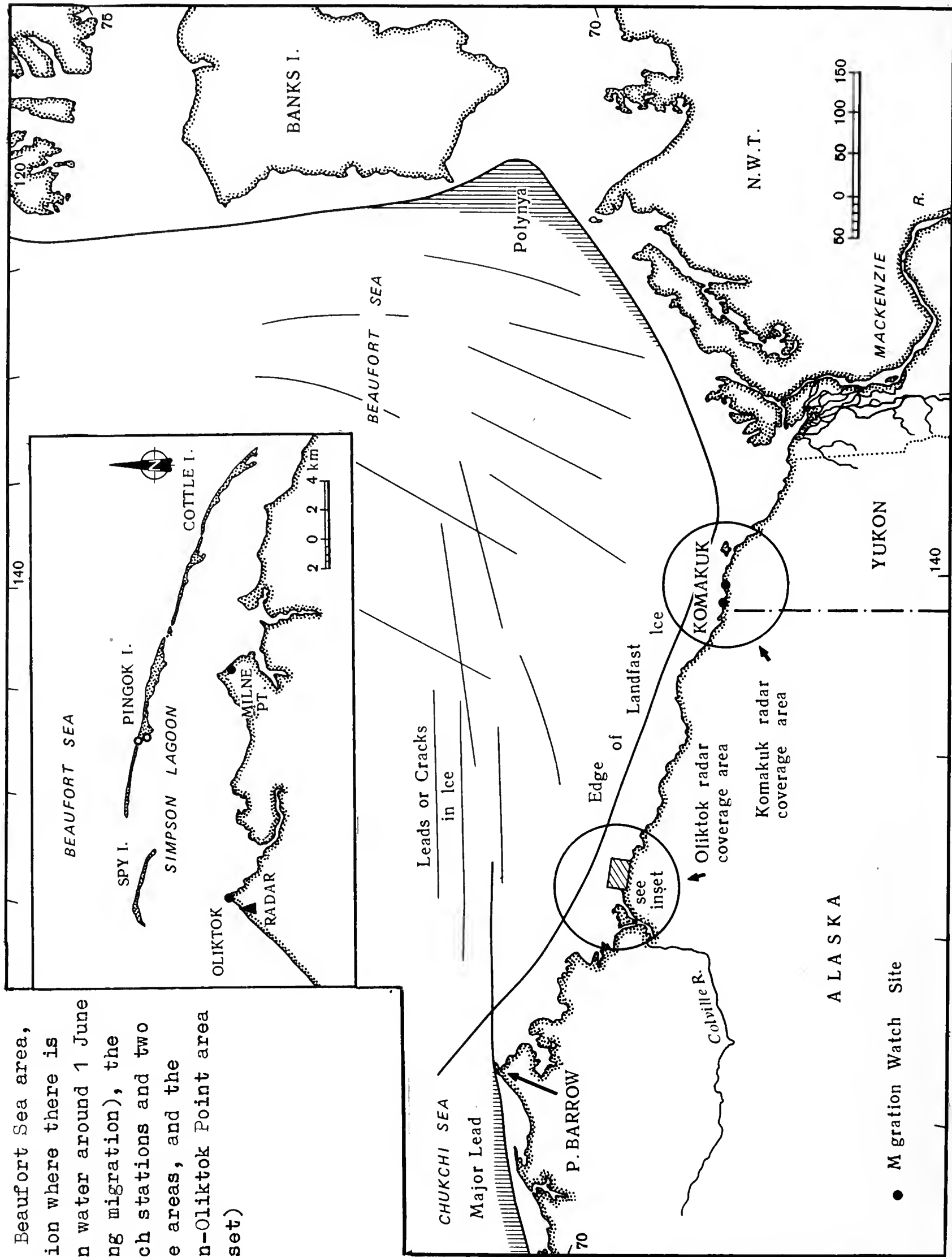
Migration and Distribution Studies

Details of the procedures used to document the numbers, movements and habitat associations of C.hyemalis along the Beaufort Sea coast are given in Johnson and Richardson (1981, 1982) and Richardson and Johnson (1981). A combination of systematic ground-based radar investigations and visual migration watches were combined with systematic aerial surveys during late May through early July of 1975 and 1977; systematic migration watches also were conducted during spring and summer of 1974 and 1978 and aerial surveys were conducted along parts or all of the coastal portions of the study area during 1973 (Gollop, Richardson, 1974) and throughout the open water period in 1978 and 1979. In 1980 and 1981, aerial surveys were conducted only during the peak of the molt in early August.

Molting and Feeding Studies

All information regarding the sex, timing and stage of molt, body condition and diet of C.hyemalis was obtained by examination of 199 specimens that were systematically collected during the open water period (July-September) in Simpson Lagoon during 1977 (90 birds in 31 collections) and 1978 (109 birds in 45 collections). During both years, samples of actively feed-

Fig. 1. The Beaufort Sea area, showing location where there is typically open water around 1 June (peak of spring migration), the migration watch stations and two radar coverage areas, and the Simpson Lagoon-Oliktok Point area of Alaska (inset)



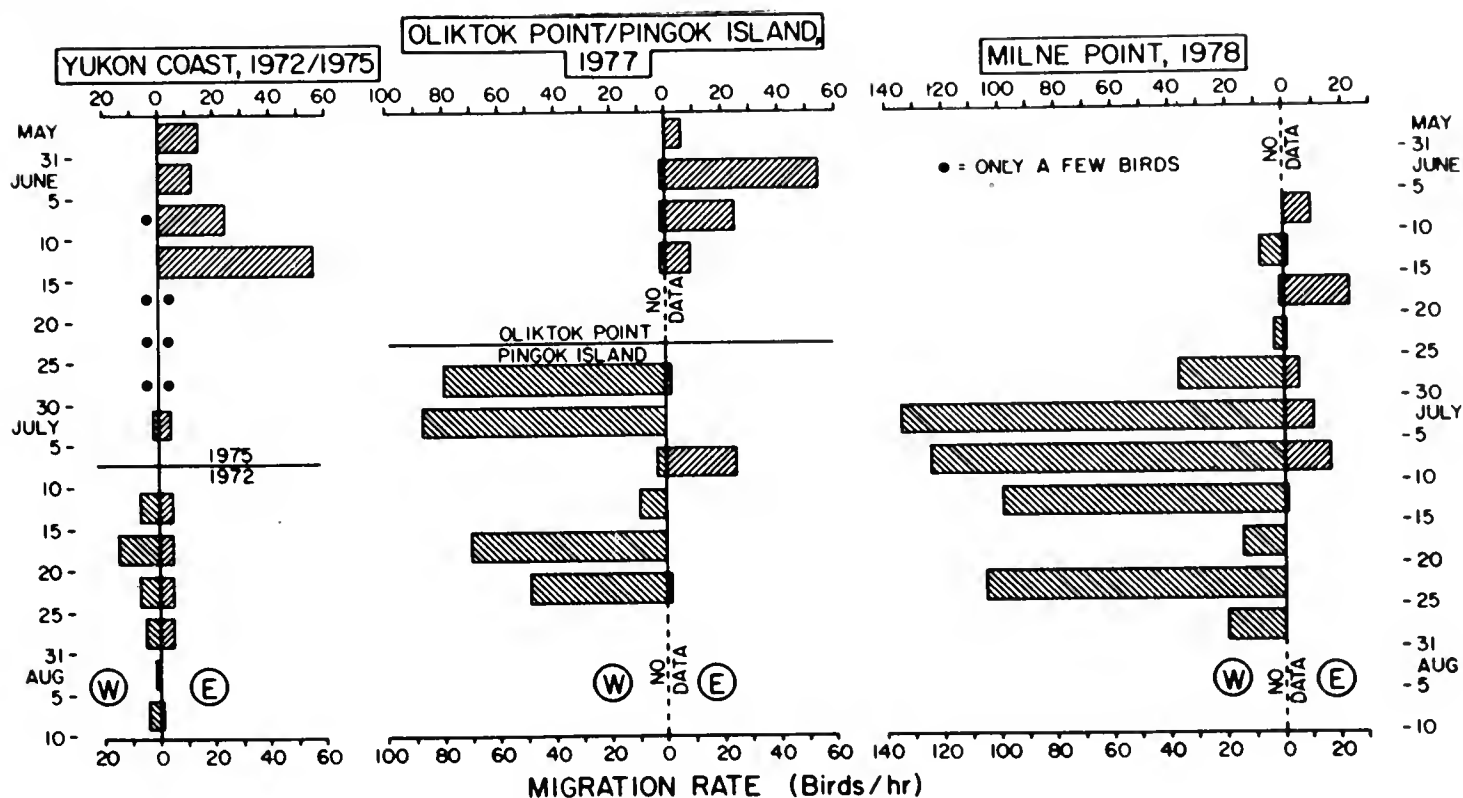


Fig. 2. Hourly rates of coastal migration by *C. hyemalis* by five-day periods in spring and summer of several years at several locations along the Beaufort Sea coast

ing *C. hyemalis* were collected to assess their diet. Concurrent collections were made of invertebrate prey available at the locations and times of bird collections. Details of the methods of the specimen collections are given in Johnson and Richardson (1981). Procedures of identification, sorting, and measuring of invertebrate organisms in bird stomachs and in the feeding habitat samples are described in Griffiths and Dillinger (1981).

RESULTS AND DISCUSSION

Molt Migration

Although the molt migrations of some waterfowl, particularly male seaducks, have been well documented (Thompson, Person, 1963; Salomonsen, 1968; Timson, 1976; Zhalakevicius, 1977), few investigators have mentioned such movements by *C. hyemalis*. Portenko (1959, 1981) and Salomonsen (1972) described northward movements by male *C. hyemalis* to molting areas in Northeast Siberia (Wrangel Island) and North Greenland, respectively. In this study the westward molt migration by *C. hyemalis* began in late June, and peaked during the first week of July, several weeks after the peak of eastward spring movements (Fig. 2). Significant westward movements of *C. hyemalis* along the Beaufort Sea coast continued until approximately 25 July in both 1977 and 1978. In 1977 when a small number (33 h) of systematic migration watches were conducted during the 16 June to 10 August period along the central Alaskan coast, 2774 birds were recorded moving west. At this same location and during the same period in 1978, when more emphasis was placed on documenting the molt migration with systematic watches (130 h), over 9000 birds were seen and over 34 000 were estimated (based on a conservative linear extrapolation) to have moved west. Most *C. hyemalis* seen flying west in 1978 before the ice left coastal lagoons were flying along shoreleads adjacent to the mainland and

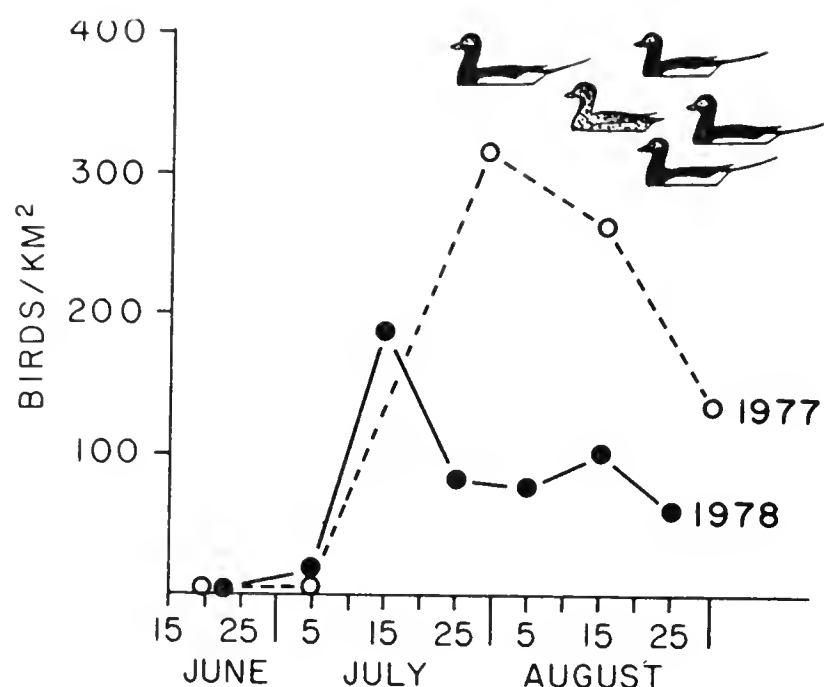


Fig. 3. Density of C. hyemalis recorded during spring and summer of 1977 and 1978 in Simpson Lagoon, Alaska

the barrier islands, or over the lagoon ice; most flew low over the open water of the lagoons after the ice retreated from these habitats in early July.

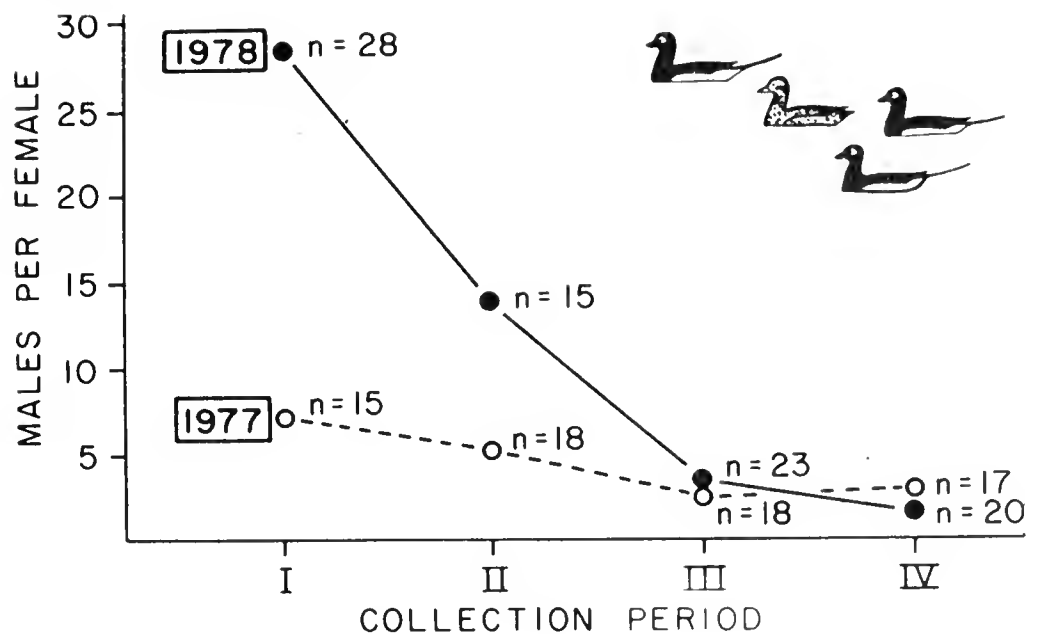
Results of the radar investigations in 1975 showed an almost continuous westward and northwestward migration of waterbirds along the Yukon and adjacent Alaska coast in late June and early July. The density of this migration within a few km of the coast (detectable during visual watches) was usually greater than densities offshore and inland, but many flocks did fly west at locations offshore far beyond the visual range of a coastal observer. Most radar echos from these westbound birds were typical of seaduck flocks. Aerial surveys offshore and nearshore in late June and July 1974 and 1975 showed that migrant C. hyemalis (plus larger numbers of migrating eiders Somateria spp. and scoters Melanitta spp.) were present there.

Use of Coastal Lagoons During the Molt

During the period of peak westward migration in 1977, shoreleads were the only open water present in coastal lagoons; during the same period in 1978, general break-up of nearshore lagoon ice had already commenced. In both years, the nearshore Beaufort Sea north of the lagoons and barrier islands remained frozen (except for shoreleads) throughout the peak period of westward molt migration. Large numbers of C. hyemalis began concentrating in the lagoons during the later part of the molt migrations. In one such lagoon that was intensively studied, Simpson Lagoon, about 1000 and 2500 C. hyemalis were recorded on 5 July of 1977 and 1978, respectively. By 15 July 1978, the number of C. hyemalis in Simpson Lagoon was estimated to be about 29 000 birds, and in late July of 1977 and 1978 the estimates were about 51 000 and 13 000, respectively.

These results suggest that during the peak of the molt migration in early July, most C. hyemalis that pass over coastal lagoons do not stop for any significant period. However, following the disappearance of lagoon ice later in July, large numbers of birds concentrated in Simpson Lagoon (Fig. 3) (Johnson and Richardson, 1981). Similar concentrations have been reported at this time in other lagoons along the north coasts of Alaska and the Yukon (Gollop, Davis, 1974; Vermeer, Anweiler, 1975; Harrison, 1977; Divoky, 1978; Johnson, Richardson, 1981; Spindler, 1981).

Fig. 4. Ratio of males to females in samples of C. hyemalis shot during four collection intervals in Simpson Lagoon, Alaska, during 1977 and 1978



Body Condition During the Molt

Approximately equal numbers of C. hyemalis were collected during four intervals in 1977 and 1978 that corresponded to the periods of pre-molt (Interval I, 17 June-27 July), peak of the molt (Interval II, 29 July-5 August), early post-molt (Interval III, 7-18 August) and late post-molt (Interval IV, 20-31 August) for males. In both 1977 and 1978 males outnumbered females by the widest margins during Interval I, when molt migrants were gathering in the lagoon (Fig. 4). During Interval II males still greatly outnumbered females, but there was a marked increase in the proportion of females as failed and/or non-breeders began arriving in the lagoons. The continued increase in the number of these females was reflected in the further decrease in numbers of males/female during collection Intervals III and IV, however, most of these decreases were the result of some males regaining flight and leaving molting areas during Intervals III and IV.

Of C. hyemalis shot in Simpson Lagoon during Interval II in 1977 and 1978 (Figure 4), 85% and 93%, respectively, were males. The abrupt decrease in the mean length of the wings of males collected in Interval II during 1977 and 1978 (Fig. 5) indicated that the period of wing molt and flightlessness by males occurred during late July-early August. Measurements of the small samples of females indicated that they molted their wing feathers later than males, during Interval III (mid-August, Figure 5) at approximately the same time that productive females (with broods) molted on tundra lakes and ponds (Johnson, Richardson, 1981:259).

Subcutaneous fat measurements of specimens collected during 1977 and 1978 indicated that male C. hyemalis were fattest during the molt period (see Fig. 5), when feather loss had reduced insulation. The subsequent loss of fat after the peak of the molt may have been caused by metabolic demands for feather replacement (Payne, 1972). The same trend may have occurred in females (especially during 1978) but too few were collected and examined to make valid comparisons.

Heterogeneity of Distribution During the Molt

Although there is circumstantial evidence that a portion of the molt migration by male C. hyemalis occurs in offshore Beaufort Sea waters (John-

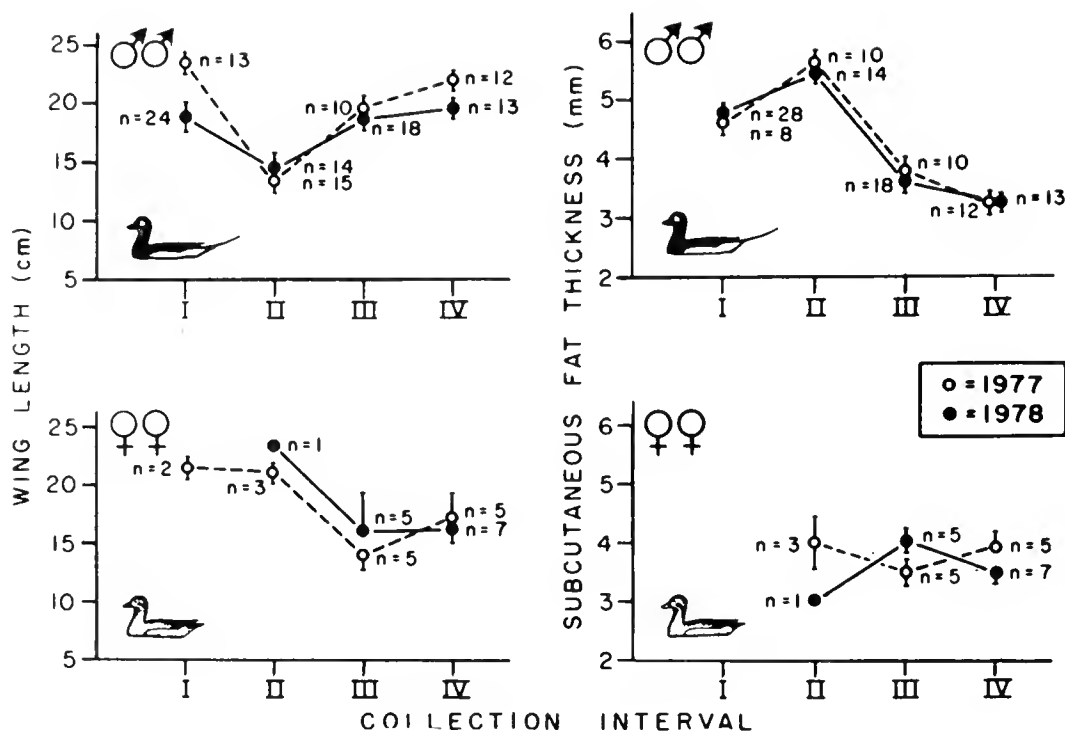


Fig. 5. Wing length and subcutaneous fat thickness of male and female C. hyemalis shot during four collection intervals in Simpson Lagoon, Alaska (mean ± S.E.)

son, Richardson, 1982), there is no evidence that a significant number may molt there. The extensive aerial surveys in offshore Alaskan Beaufort Sea waters by Harrison (1977) and the limited coverage in offshore waters during our studies have not documented molting C. hyemalis nor any other seaducks there.

On the contrary, males concentrated in high densities in specific lagoons (and a few large tundra lakes) during the molt period. The degree to which these ducks are associated with barrier islands during the molt period is remarkable. During 1977, over half of all C. hyemalis recorded during aerial surveys in Simpson Lagoon were associated with the south shores of the barrier islands. In 1978, the distribution of molting C. hyemalis in the lagoons was more intensively investigated; approximately 90% of all birds recorded during the surveys were within 400 m of the south shores of the islands. Distributions of male C. hyemalis relative to the barrier islands were directly related to the direction of the prevailing winds (Fig. 6); during periods of strong winds from the north, most birds were observed in the lee (± 400 m S) of the barrier islands. Strong winds with a northerly component prevail along the north coast of Alaska during the July through September period (Brower et al., 1979; Kozo, 1979) and the barrier islands apparently provide protection for C. hyemalis from these winds and associated rough water. Other studies during the male molt period (Johnson, 1982a) have documented more conclusively the relationship between wind speed, wind fetch and wave height north and south of the barrier islands and have shown that when they are not feeding in nearby lagoons, C. hyemalis spend a significant amount of time roosting on the leeward beaches or loafing in adjacent shallow waters behind the relatively predator-free barrier islands.

Diet and Prey Selection During the Molt

Concurrent with break-up and the disappearance of ice from coastal lagoons along the Beaufort Sea, these areas are repopulated by dense concentrations of a few species of abundant epibenthic crustaceans - mainly amphipods and mysids (Griffiths, Dillinger, 1981). Three species, the amphipod Onisimus

glacialis and the two mysids Mysis litoralis and M. relicta, comprised the majority of organisms in epibenthic habitats where feeding C. hyemalis were collected in 1977 and 1978. Correspondingly, these three species comprised the bulk of the diet of C. hyemalis in 1977 and 1978 (Fig. 7). The sampling programs in both years were designed to determine not only the diet of C. hyemalis but also the availability of prey in various strata of lagoon waters. The standing stocks of invertebrate prey in Simpson Lagoon during 1977 and 1978 always remained at least one or two orders of magnitude greater than the daily energy requirements of the populations of C. hyemalis present there (Griffiths, Dillinger, 1981; Johnson, Richardson, 1981:342).

Although feeding C. hyemalis were largely opportunistic - they fed on the predominant prey species available - they were highly selective in the size of prey consumed (Johnson, 1982b; Fig. 8). Furthermore, in Simpson Lagoon they appeared to be more effective (had fuller stomachs) when feeding in areas where epibenthic prey were most dense (Fig. 9, Johnson, Richardson, 1981:333-335).

SUMMARY AND CONCLUSIONS

Long-tailed Ducks show a remarkable degree of adaptation in their use during the molt period of a narrow band of shallow lagoon habitat along the coast of the Beaufort Sea. The occurrence and timing of the molt migration by males roughly coincides with the disappearance of ice and the availability of open water in lagoon habitats. During the molt period, males (and some females) concentrate in protected lagoons. They are fattest during the peak of the molt prior to feather replacement. Their local distributions are strongly clumped along the south shores of the barrier islands where they roost, where they are afforded protection from predators and rough water and have easy access to dense concentrations of highly available food in the nearby lagoons. The species composition of their diet is very similar to that found in the epibenthos where they feed; in this regard they are opportunistic. However, they show a high degree of selectivity in that they appear to prey on individuals significantly larger than the average size found in their feeding habitats. Furthermore, most of the birds feed in relatively deep lagoon waters where epibenthic prey are most dense and where the birds apparently prey more effectively.

Major causeways, artificial islands and increased boat and aircraft traffic associated with petroleum development along the Beaufort coast are facts-of-life. A major spill of toxic materials fortunately has not yet occurred nor have there been extensive alterations in barrier island configuration nor of nearshore circulation patterns. However, industrial development is progressing at a very rapid rate in this area. Government, industry and native organizations are currently sponsoring a wide variety of research to determine the effects of this development. The Long-tailed Duck is one of a few key species whose use of nearshore waters in the Beaufort Sea is being carefully monitored.

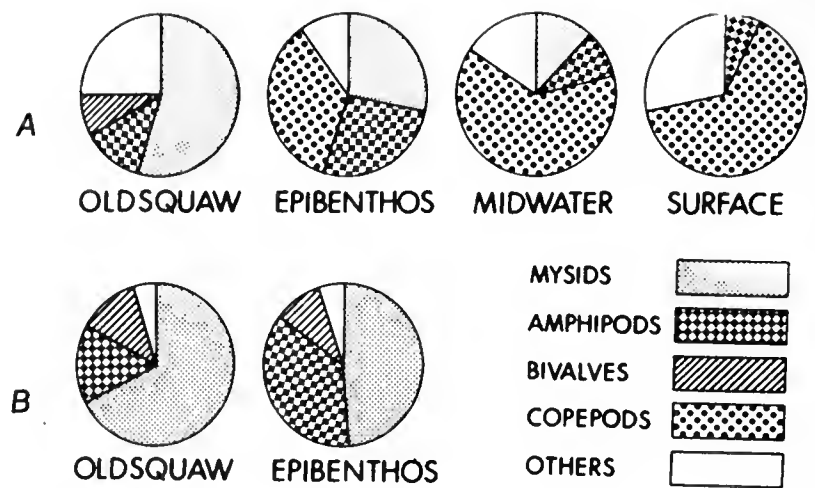
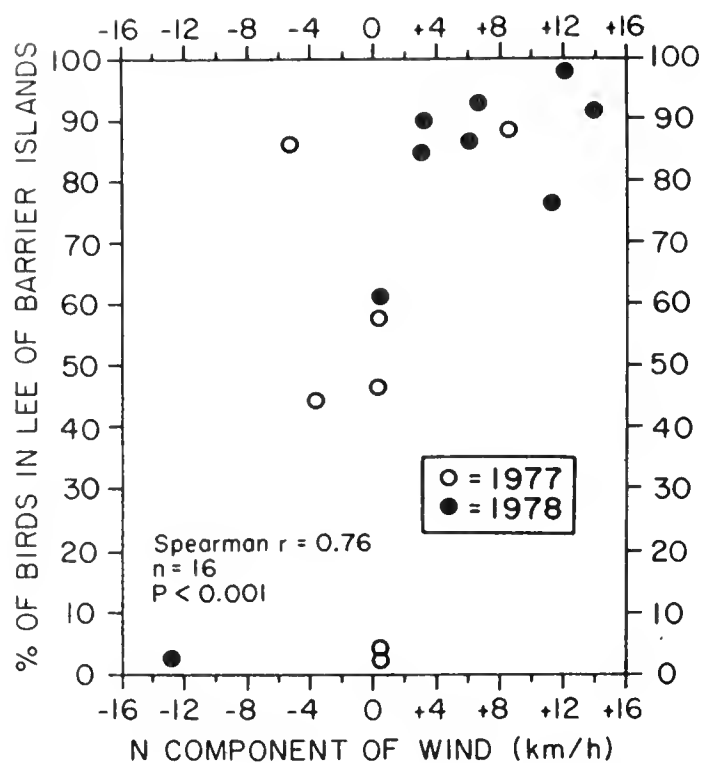


Fig. 7. Volumetric composition of *C. hyemalis* diets and feeding habitat samples in Simpson Lagoon, Alaska. A - 1977, B - 1978

Fig. 6. Relationship between wind direction and speed (component) and the distribution of *C. hyemalis* near barrier islands in the Simpson Lagoon area of Alaska

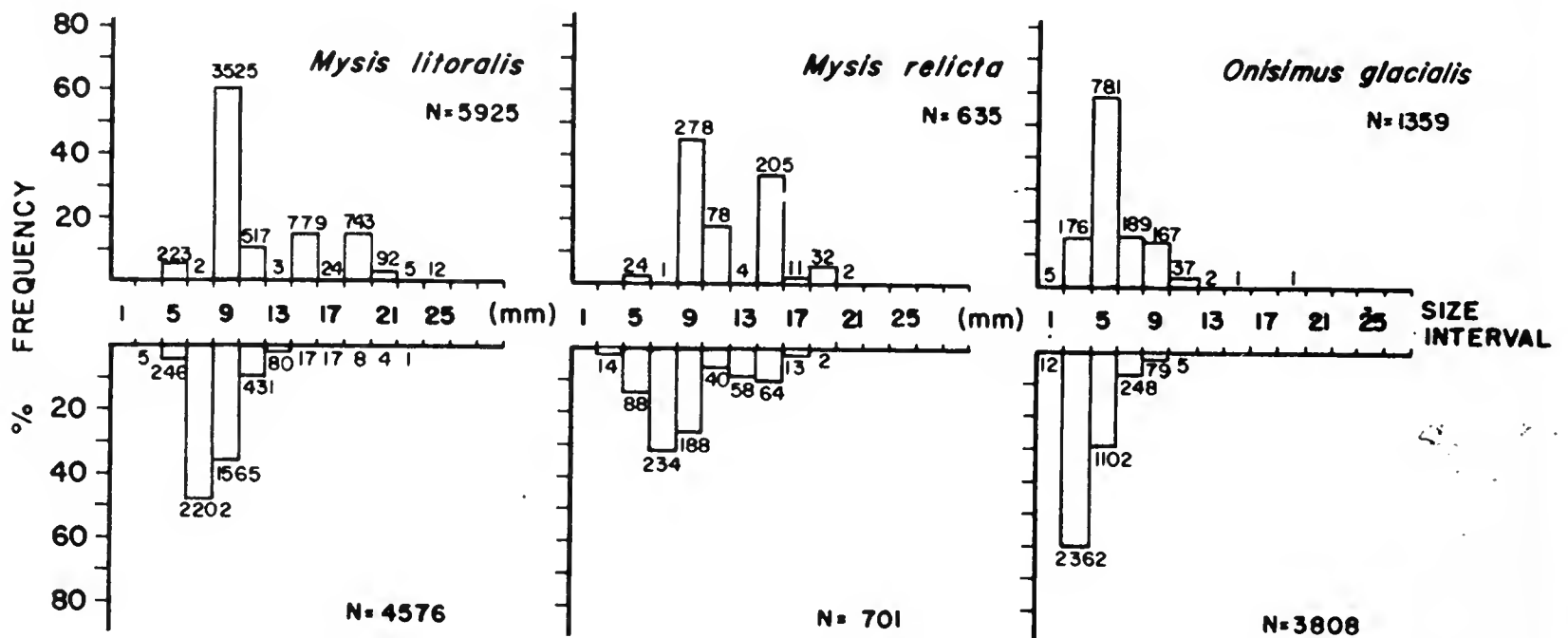


Fig. 8. Distribution in Simpson Lagoon of sizes of prey in stomachs of feeding *C. hyemalis* and in the epibenthos where feeding *C. hyemalis* were collected. Upper diagram - oldsquaw stomachs, lower diagram - oldsquaw feeding habitats

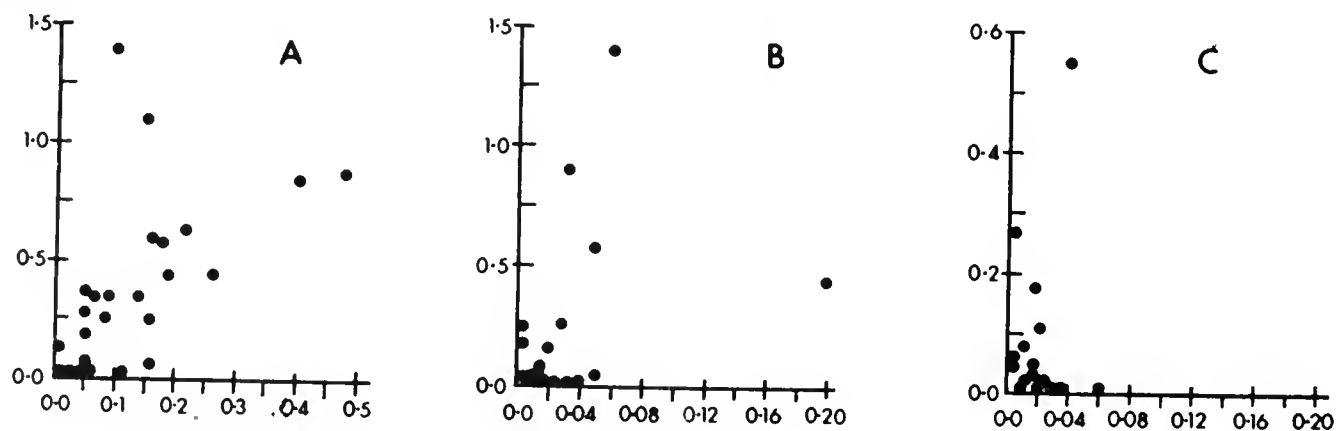


Fig. 9. Relationship in Simpson Lagoon in 1978 between amount of prey in stomachs of feeding *C. hyemalis* and the biomass of prey in the epibenthos where feeding *C. hyemalis* were collected; $n = 25$. A - total Invertebrates: $r_{\text{rank}} = 0.68$, $p = 0.001$; B - total Mysids: $r_{\text{rank}} = 0.34$, $p = 0.02$; C - total Amphipods: $r_{\text{rank}} = 0.02$, $p = 0.10$. Ordinata - amount in oldsquaw stomachs, g dry weight; abscissa - biomass in epibenthos, g dry weight/m²

ACKNOWLEDGEMENTS

Our work on Long-tailed Ducks in the Alaskan Beaufort Sea (Johnson, Richardson, 1981) was supported through the Outer Continental Shelf Environmental Assessment Program (OCSEAP) of the National Oceanic and Atmospheric Administration (NOAA), U S. Department of Commerce, and the Bureau of Land Management, U S. Department of Interior. The support of the OCS Arctic Project Office helped immensely; special thanks go to Drs. David Norton and Gunther Weller of that office.

Many people at LGL helped in the field and office. In particular, LGL studies of fish and invertebrates in Simpson Lagoon were relevant to the methods and results of these other studies. My thanks go to Chip Welling, Gary Searing, William Griffiths, Peter Craig, Lew Haldorson, Howard McElderry and Rob Dillinger.

John Richardson has helped in many ways throughout this research; he, Eric Tull, Jeff Green, Gary Searing and Declan Troy of LGL kindly reviewed earlier versions of this paper. Diane Hollingdale prepared the figures.

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POPULATIONS AND BREEDING SCHEDULE OF WADERS IN HIGH ARCTIC GREENLAND

Hans Meltofte

Zoological Museum, Universitetsparken, DK-2100 Copenhagen O, Denmark

Waders are the dominating birds of the high arctic tundra of Greenland, both regarding population density and number of species. Ten species of waders breed in high arctic Greenland, while only two breed in significant numbers in the low arctic part. This is related to the highly different ambient conditions in the two regions. Low arctic Greenland is covered by an often meter-deep and complete snow cover until late spring, and the vegetation is relatively luxuriant and scrub-like. In contrast to this, high arctic Greenland has a much lower precipitation and the snow is blown off on large areas. The vegetation is extremely low and often sparse. Even within the high arctic zone, there are local and annual differences in these respects, all reflected in the timing of the breeding and the population densities of waders. Feeding conditions during the pre-laying and laying periods may be a limiting factor to the populations and may even determine the timing of the breeding. Predator efficiency is probably a decisive factor too, in areas with great snow cover. The waders apparently arrive a few days earlier nowadays than in the turn of the century, which may be related to changes in spring snow cover since then.

Finn Salomonsen

Zoological Museum of the University, Universitetsparken 15, DK-2100
Copenhagen Ø, Denmark

Since low temperature is one of the properties of high altitudes the conservation of energy is a vitally important problem for mountain organisms. The homiotherms have active internal thermogenesis which maintains a steady pattern of body heat, and the problem dealing with cold climate is, therefore, to avoid an excessive loss of heat from the peripheral and distal parts of the body. In birds these problems are mainly solved by insulation and by certain adjustments of body size and body proportions.

In warm-blooded animals of northern latitudes, particularly those of the Arctic region, the most wide-spread measure to reduce heat loss is an increase in body size. The physiological reason for this is the fact that in larger organisms the surface is comparatively reduced and the heat loss to the surroundings, therefore, relatively smaller. This very well-known and commonly manifested ecogeographical rule is known under the designation Bergmann's rule. The evidence for the existence of this rule in birds and mammals is so extensive that a closer description is unnecessary. Huxley (1942) is of the opinion that Bergmann's rule applies in 70 to 90 per cent of all relevant bird species. I may further refer to Hamilton (1961) and Salomonsen (1972). It is noteworthy that Bergmann's rule is even apparent in certain historically sedentary populations of Homo sapiens, as documented by Schreider (1957).

The physiological explanation of this rule has been questioned by several students, first of all by Scholander (1955, 1956), but has been defended by Mayr (1956) and Hamilton (1961). Scholander's view-point was that the differences in size involved were too small to provide significant heat conservation. It is not possible, however, to regard this rule as functional in an isolated state independent of all other adaptations. These assume many forms, since the homiothermous animals have different means of adaptations to the cold available. All these adaptations must be regarded as a common unit since as a rule climatic adaptation involves multiple adaptive responses. Hamilton (1961) in particular has emphasized the theory of multiple evolutionary pathways for achievement of heat economy. He has in this way convincingly demonstrated that the conceptual schism between physiologists and evolutionists on the topic of the adaptive meanings of Bergmann's rule, and also of other ecoclimatic rules, is more apparent than real.

Just as in northern latitudes the adaptations of birds to high altitudes is controlled by Bergmann's rule, demonstrating an increase in size correlated with ascending altitude. The temperature decreases by about $1/2^{\circ}\text{C}$ for every 100 m altitude. This decrease gives rise to a series of different plant formations, from deciduous vegetation (or tropical growth) in the lower altitude, followed by coniferous forests up to the tree-limit, and above it, on particularly high mountains, alpine grassland, followed by a nivale zone of snow and glaciers.

The increase of size in birds with growing altitudes has been described

by various students, first by Salomonsen (1934), who analyzed the Madagascar mountain avifauna, further by Rand 1936 (New Guinea), Mayr 1942 (tropical mountains), Mayr 1944 (Timor Island), Traylor 1950 (Bolivia), Chapin 1932 (Zaire), Mayr 1963 (general remarks), Hamilton 1961 (general remarks).

Salomonsen (1934) in his Madagascar paper mentioned above gave the following explanation of the increase in size with altitude, an explanation which I still hold to be the most plausible: "The larger size of the mountain-birds is probably a reaction against the lower temperature on the places at high altitudes. The waste of heat, caused by the radiation from the outer surface of an organism, is proportional to the area of the surface and to the difference between the temperature of the organism and the atmosphere. To keep the inner temperature of a homeotherm animal at the normal height (in a bird about 42° C.), the organism, when living in a cold climate, is forced to augment its heat-capacity. An increased production of heat, however, is very troublesome or even perilous for the avian organism, and it therefore reduces the amount of heat lost to the atmosphere by diminishing the outer surface. The only method by which this can be undertaken in a bird is to increase the volume of the body; the larger the bird grows the smaller (comparatively) will be the surface, and on account of this the percentage of heat lost to the atmosphere will decrease (Bergmann's rule)."

The conditions for developing populations or subspecies with increasing size in mountains appear to vary very much, not only from species to species, but also from one geographical area to another. In tropical mountains the tendency is much more pronounced than in the holarctic area. The reason for this is probably the fact that most tropical populations are much more stationary than those living in the temperate zones. It is a well-known fact, for instance, that tropical sedentary species are unable to cross even narrow water-gaps only a few km broad. The same situation is apparent in the mountains. In the tropics the selection pressure caused by the decreasing temperature is able to influence the populations for full scope without interference from neighboring populations the gene-pools of which elsewhere would mix with that of the population in question and reduce or invalidate the effect of the selection.

Another condition has something to do with the height and the area of the mountain range. If the mountains are not sufficiently elevated the selection-pressure will be too weak, although it has a slight effect in tropical stationary bird populations even on modest elevations. The same may be said if the area of the mountain range is moderate. In temperate regions there will in such cases be a wholesale mixing with adjacent populations which are unaffected by the selection-pressure in the high elevations. Again here it must be emphasized that tropical stationary populations are very modest in their requirements for producing increased size.

Finally, it appears usually to be a condition that the species in question has an altitudinal distribution along an essential part of the mountain slopes, preferably from the lowland to the tree-limit or to the highest peaks.

I shall give some examples of the importance of these conditions. On the

comparatively small Timor Island (32.000 km²) with the highest mountain about 3.600 m, collecting has been done only to 2.500 m altitude. Even this modest height influences the body proportions of the birds inhabiting the mountains. According to Mayr (1944) two males of Gerygone inornata from 160 m altitude had a wing-length of 48 and 52.2 (average 50.1) mm, while six males from 2.000-2.300 m measured 54-56 (average 55.1) mm. This is a difference of the average wing-length of 5 mm or an increase per 100 m of 0.25 mm or 0.50 per cent of the average wing-length of the lowland population¹. Compared with examples from other areas this appears to demonstrate an appreciable increase in size. In Phylloscopus presbytes the average wing-length in males at 300 m was 54.3, and at 2.000-2.300 m 58.5, which means an ASI-Index of 0.42.

Even bird populations living at rather low elevations may show an influence of the decreasing temperature by increasing their wing-length. In Dicaeum maugei the wing-length in males at 0-160 m altitude was on an average 55.3 mm, at 1.100-1,200 m it was 56.9 mm, i.e. an ASI-Index of 0.29. As a final example can be mentioned Geopelia striata, in which males had an average wing-length at sea-level of 105.5 mm and already at 300 m a wing-length of 107.0 mm, which means that it had an ASI-Index of 0.48. Mayr adds that in all the species in which the material was sufficient to demonstrate differences in body proportions with increasing elevations it involved an increase in size with altitude.

The situation in the tropical mountains of Timor, described above, differs remarkably from that in the mountain areas in Holarktis. In Europe the mountains are much higher and cover a much larger area than those of Timor, the mightiest mountain chain being that of the Alps with peaks reaching 4.000-4.800 m. Still, with the exception of Parus montanus (nominate montanus) no mountain species in Europa has developed forms with greater wing-length than the lowland forms. An attempt to explain this extraordinary phenomenon has been given above. The few mountain subspecies of European birds are all characterized by coloristic features. Most of them are totally isolated from the lowland forms. This is particularly characteristic of the so-called boreomontane species. They have their main distribution in the northern boreal region (the Taiga region), but are found also in the central European mountains in the subalpine zone covered with coniferous vegetation. They are widely isolated from the boreal populations. A good example of these species is Picoides tridactylus alpinus, which is found only in the subalpine zone, which in the Alps covers the altitudes from 1.400 to 2.400 m (Blotzheim 1962). Nucifraga caryocatactes is another example of the boreomontane birds, restricted to the subalpine zone and isolated from the boreal lowland form. This species has not developed any morphological differences whatsoever between the lowland and the isolated mountain population which both belong to the same subspecies.

¹ The increase in the average wing-length per 100 m expressed in per cent of the average wing-length of the lowland population is used in the following as a standardized measure in order to compare the altitudinal size increase of various tropical species in different continents. The figure is called "Altitudinal Size Increase Index", abbreviated to ASI-Index.

Other European mountain species belong to the so-called paleomontane faunal type and have had their origin in the alpine zone of the high Palearctic mountains (cf. Salomonsen, 1972). Two paleomontane species should be mentioned, of which the mountain populations form the subspecies Anthus spinoletta spinoletta and Eremophila alpestris balcanica. They are found only in the alpine zone which in the Alps covers 2,400-4,000 m (von Blotzheim, 1962) and are totally isolated from the boreal and arctic forms Anthus spinoletta petrosus and Eremophila alpestris flava.

All these characteristic mountain birds of Europe have an altitudinal distribution of only 1,000-1,600 m, and this modest altitudinal amplitude appears to be too small to influence these birds, which probably mix completely in their entire mountain range. It is also quite natural that they do not show any size increase compared with their northern lowland populations, because the temperature conditions in the alpine-subalpine zones in the mountains must be supposed to be very similar to those in the arctic-boreal regions in the north.

In the enormous central Asiatic highland, covering mountains and tablelands extending from Afghanistan, Pamir and Karakorum through Sinkiang, Altai, Kun Lun to the Tibetan plateau, Himalaya and Yunnan, there are excellent conditions for developing mountain forms with greater body-proportions. The area covered is extremely large as a matter of fact the largest in the world. The altitudes are also very large, in Himalaya attaining higher elevations than any other area in the world. A great number of birds are distributed from the European and Siberian lowland right to the higher parts of the Asiatic highland. A few examples will show the extreme influence of the mountain climate in those areas for the variation of size in birds.

In Pica pica, distributed in the greater part of the Holarctic (except in the Arctic region), the size variation is very pronounced. In the northern boreal region there are large forms, according to Bergmann's rule, fennorum in N.E. Europe with a wing-length of 190-221 (average 204.0) mm, and the Siberian forms hemileucoptera, leucoptera and bactriana being slightly larger (wing-lengths 210-227 mm). The temperate lowland of Europe is inhabited by nominate pica, which is smaller than the northern forms, with a wing-length of 183-202 (average 190.0) mm. In North Africa a still much smaller form, mauretanica, is found; wing-length 152-172 (average 163.0) mm. To be sure, there are other subspecies in Europe and northern Asia, but they do not in their body-proportions deviate from the general picture here described. However, in Himalaya and S.E. Tibet the Magpie has developed into a huge form, bottanensis, with a wing-length of 244-265 (average 253.00) mm (Vaurie, 1959). It is noteworthy, that the increase in average wing-length from temperate Europe to northeastern boreal Europe is only 14 mm, while it is no less than 49 mm from the temperate lowland to Himalaya. This demonstrates how significant the selection pressure (by environment) is in the highland of Asia.

Exactly the same development has taken place in another Corvid of wide distribution. Corvus corax is ranging through the entire Holarctic and is in northern N. America as well as in Greenland represented by the subspecies

principalis which extends even into the higharctic zone as a breeding bird. Its wing-length is 440-475 (average 455.0) mm. Somewhat smaller forms are found in eastern Siberia (kamtschaticus) and in the mountainous W.S.Asia, eastwards to Afghanistan and Kashmir (subcorax). In Europe and the southern parts of Siberia, eastwards to Lake Baikal, nominate corax is found, with a wing-length of 375-442 (average 414.0) mm, and in Himalaya and Tibet (above 4.000 m altitude) tibetanus with the wing measuring 470-490 (average 479.0)mm (Vaurie, 1959). The increase in the average wing-length from the arctic principalis to nominate corax from the boreal and temperate Palearktis is 41 mm, while it is 65 mm from the temperate Palearktis to Himalaya. The development of the body proportions is thus the same in the Raven as in the Magpie.

Generally, Bergmann's rule holds good of a large number of mountain birds of Highasia. There are numerous examples of species with larger body proportions in these areas. I shall content myself in mentioning only the species belonging to two families. In Alaudidae the following species have subspecies with larger proportions in the mountains of central Asia: Alauda gulgula, Galerida cristata, Eremophila alpestris and Calandrella acutirostris; in Corvidae: Pyrrhocorax pyrrhocorax, Pyrrhocorax graculus, Pica pica, Corvus macro-rhynchus, Corvus corone and Corvus corax.

On the southern side of Himalaya where the avifauna is mostly of oriental origin, there are no subspecies with increased body proportions in the upper parts of the Himalayan slopes. The reason for this fact is undoubtedly the small vertical amplitude in the distribution of the mountain birds. There are no species distributed from the lowland to the alpine zone of the mountains, a few reach 3.000 m in their vertical range, most only 1.000-2.000 m, 40 species less than 1.000 m and 20 species even less than 500 m (Diesselhorst, 1968).

It may seem peculiar that many of the large mountain forms of central Asia have extended their distribution to lower mountains which are not higher than the central European ones where no size variation was found. However, the considerable height extending over large areas lowers the ambient temperature markedly, and in this way the selection pressure is so strong that the organisms respond by developing large body proportions. The superior size then radiates to the populations inhabiting lower altitudes through mixing of the gene-pools.

The situation in Madagascar resembles that in Timor, although the country has a much larger area. The highest mountain, Tsaratanana, reaches an altitude of 2.880 m. The mountains form a central high-plateau, not as a continuous area but with a number of scattered separate peaks and plateaus. of which the most important ones are the massives Ankaratra, Tsaratanana, Mt. d'Ambre and Betsileo. There are only two genuine mountain birds in Madagascar (Sarothrura watersi and Dromaeocercus seebohmi), but a number of lowland birds inhabit the mountains, at least to 2.000 m; no collecting has been done at higher elevations; cf. Rand, 1936a:243 on the mountain species and subspecies. In Table 1 a number of birds are enumerated which range from the lowland up the mountain slopes, all showing a distinct development of greater size with altitude. Almost all mountain specimens were secured at a place cal-

T a b l e 1. Wing-length (in millimeters) of populations of mountain birds in Madagascar, based on Salomonsen (1934)
n: number of specimens examined, altitude in m, average measurements in brackets

| Populations | Altitude | Wing-length | n | ASI-Index |
|-------------------------------|----------|------------------|-----|-----------|
| Newtonia b.brunneicauda | 0 | 52-58 (55.03) | 126 | |
| Newtonia b.monticola | 1.800 | 58-62 (59.48) | 19 | 0.45 |
| Zosterops m.madaraspatana | 0 | 52-59 (56.05) | 150 | |
| Zosterops m.analoga | 1.800 | 59-65 (61.83) | 16 | 0.57 |
| Saxicola torquata sibilla | 0 | ♂♂ 64-71 (67.31) | 45 | |
| Saxicola torquata sibilla | 0 | ♀♀ 63-67 (65.35) | 26 | |
| Saxicola torquata ankaratrae | 1.800 | ♂♂ 73-76 (74.44) | 7 | 0.59 |
| Saxicola torquata ankaratrae | 1.800 | ♀♀ 73-74 (73.40) | 5 | 0.68 |
| Monticola imerina salomonseni | 0 | ♂♂ 75-80 (77.43) | 23 | |
| Monticola imerina salomonseni | 0 | ♀♀ 71-78 (74.53) | 15 | |
| Monticola imerina sharpei | 1.800 | ♂♂ 80-87 (83.10) | 10 | 0.41 |
| Monticola imerina sharpei | 1.800 | ♀♀ 79-84 (81.60) | 5 | 0.53 |
| Nesillas typica ellisii | 0 | ♂♂ 57-68 (62.06) | 64 | |
| Nesillas typica ellisii | 0 | ♀♀ 56-65 (59.49) | 39 | |
| Nesillas typica monticola | 1.800 | ♂♂ 66-72 (68.77) | 13 | 0.60 |
| Nesillas typica monticola | 1.800 | ♀♀ 64-67 (65.50) | 4 | 0.56 |

led Monjakatampo in the Ankaratra Mountains at 1.800 m altitude, and this is the altitude used in Table 1 to calculate the ASI-Index. The nomenclature of the forms mentioned is just as in Salomonsen 1934, with the exception of Monticola imerina. It appeared that the type-specimen of the wide-spread bird of the lowland, known as Monticola i. sharpei, is in reality a specimen of the mountain race. My suspicion about its origin was already aroused in my paper 1934 and I referred to it as being "exceptionally big". Farkas (1973) has shown that the type actually belonged to the mountain form, which therefore has to be called M.i.sharpei, while he gave a new name (salomonseni) to the lowland form.

It appears from Table 1 that the ASI-Index is rather similar in the different species, usually about 0.40-0.60. This is about the same figure which was found in the Timor birds, mentioned earlier in this paper, although generally somewhat higher.

Turning to Africa, one of the most thorough studies on size variation and its connection with altitude was made by Moreau (1957) on the genus Zosterops, based on a very large material. Unfortunately, he mixed all taxa together giving all measurements in a common scheme (Appendix 3) in which all African and Indian Ocean species were combined. However, by using his checklist of the African forms (Moreau, 1967) it is possible to arrange his many populations into the proper species. In Table 2 a number of populations of the wide-spread species Zosterops senegalensis have been enumerated. Mo-

T a b l e 2. Wing-length (in millimeters) of mountain populations of Zosterops senegalensis, based on Moreau(1957)
n: number of specimens examined, altitude in m, average measurements in brackets

| Populations | Altitude | Wing-length | n | ASI-Index |
|-------------------------------------|----------|----------------|----|-----------|
| Zosterops senegalensis polioogastra | 2.400 | 58-69 (63.9) | 54 | 0.86 |
| Zosterops senegalensis polioogastra | 1.800 | 59-63 (61.5) | 11 | 0.90 |
| Zosterops senegalensis kaffensis | 2.400 | 61-65 (63.2) | 14 | 0.81 |
| Zosterops senegalensis kaffensis | 1.950 | 57-63 (60.0) | 29 | 0.67 |
| Zosterops senegalensis senegalensis | 150 | 51-55 (53.5) | 18 | 0 |
| Zosterops senegalensis senegalensis | 450 | 53-59 (55.9) | 23 | 1.49 |
| Zosterops senegalensis senegalensis | 450 | 51-57 (53.7) | 19 | 0.12 |
| Zosterops senegalensis kikuyuensis | 3.000 | 59-66 (62.0) | 23 | 0.56 |
| Zosterops senegalensis kiruyuensis | 2.250 | 56.5-64 (60.6) | 95 | 0.62 |
| Zosterops senegalensis mbuluensis | 1.650 | 58-63 (60.4) | 14 | 0.86 |
| Zosterops senegalensis mbuluensis | 1.950 | 60-67 (62.5) | 37 | 0.93 |
| Zosterops senegalensis winifredae | 1.650 | 58-62 (59.1) | 12 | 0.70 |
| Zosterops senegalensis jacksoni | 2.100 | 58-65 (60.6) | 45 | 0.68 |
| Zosterops senegalensks jacksoni | 2.550 | 57-67 (62.0) | 68 | 0.66 |
| Zosterops senegalensis jacksoni | 2.100 | 57-65 (60.6) | 17 | 0.68 |
| Zosterops senegalensis anderssoni | 1.200 | 57-63 (59.9) | 43 | 1.14 |
| Zosterops senegalensis anderssoni | 1.140 | 56-62 (59.4) | 51 | 1.11 |
| Zosterops senegalensis anderssoni | 1.740 | 59-63 (61.0) | 18 | 0.88 |
| Zosterops senegalensis anderssoni | 1.350 | 57-62 (59.3) | 19 | 0.90 |
| Zosterops senegalensis anderssoni | 1.200 | 55-62 (58.6) | 48 | 0.91 |

reau has given the altitudes in feet, but I have transscribed them into meter. The ASI-Index is generally considerable, still larger than in the Madagascar birds. However, the only population studied from very high mountains (kikuyuensis from 3.000 m) have an ASI-Index slightly smaller than the usual type, only 0.56, the same as Zosterops madaraspataana analoga from Madagascar. However, Moreau's figures cannot be compared with those from other tropical countries, mentioned above. The measurements have been taken on very scattered populations, inhabiting different mountains, often far apart, and many populations may be quite isolated. Even within the single species senegalensis there may be local conditions or special environmental or biological factors influencing the size variation. It is peculiar, for instance, that two populations of nominate senegalensis differ extremely much in their ASI-Index, in spite of the fact that they inhabit the same altitude (450 m), one having an index of 0.12, the other of 1.49.

Chapin (1932) has analyzed the mountain bird fauna of Africa, particularly that in Zaire. The mountain fauna is rich in species, but these are specifically distinct from their nearest allies in the adjacent lowlands. There are only few cases in which a lowland bird (among passerines, of the stationary type) has penetrated the highland forests and given rise to a

particular mountain subspecies. Chapin mentions only six such cases. The distinctness of the mountain species shows how difficult it is for lowland birds to enter the higher forests. Birds of the equatorial forests range from sea-level to about 1.500 m altitude with no differences, but a little up almost the whole bird fauna may be replaced, especially if there are forests (Chapin, 1932).

A few species are exclusively alpine in Zaire. These are some sunbirds, some species of Seicercus and the Alpine Swift, Apus melba. The latter has a wide distribution in the subtropical lowland of Europe and western Asia, but the African populations have much bigger proportions than the lowland form. The latter has a wing-length of 205-230 mm, while A.m.maximus of Ruwenzori Mountains measures 231-236 mm. The well-known sunbirds Nectarinia tacazze and N.johnstoni of all the high mountains of East Africa are characteristic of being much larger than the numerous lowland sunbirds. The big size of the genuine mountain birds must undoubtedly be interpreted in the same way as that of the local mountain subspecies, namely as an adaptation to the low temperature during the evolution of these species.

Even in New Guinea the mountain bird fauna is rich in species. Just like in Africa there are genuine highland birds which are considerably larger than their closely allied lowland congeners, from which they differ mainly in their bigger proportions, whereas their coloration is similar. Among the most well-known examples the following shall be mentioned: Halcyon torotoro distributed between 450 and 900 m altitude and its highland representative H.megarhynchus from 750 to 2.100 m; Peltops blainvillii up to 480 m altitude and P.montanus from 750 to 2.700 m, and finally Ptiloprora guisei from 1.170 to 2.500 m and P.perstriata from 1.650 to 3.600 m altitude. The altitudes are quoted from Rand and Gilliard (1967).

Many species are distributed from the sea level along the mountain slopes to the highland, and in several cases they have developed special mountain forms. Mayr and Rand (1935) have described three such mountain forms from Southeast New Guinea, and in all cases the mountain form is larger than the lowland subspecies. In the game-bird Synoicus ypsilophorus they described a form (mafulu) from the mid-mountain grassland from about 1.000 to 2.000 m altitude with wing-length in adult males of 90-97 (average 93.4) mm, compared with 85-94 mm in the lowland form plumbeus. In the alpine region above 2.800 m another new form (monticola) is distributed. It is still larger, with a wing-length in males of 104-109 (average 107.3) mm. When using the average altitude of the range of mafulu (1.500 m) it is possible to calculate the ASI-Index of monticola compared with mafulu, which has the considerable size of 1.15.

In Malurus alboscapulatus mafulu from 1.000 to 2.000 m altitude the wing-length in adult males is 48-51 (average 49.2) mm, compared with 45-47 mm in the lowland form naimii. The ASI-Index is approximately 0.46. The third form described by Mayr and Rand is Megalurus timoriensis macrurus from the alpine grassland above 2.800 m, with a wing-length in adult males of 70-76 (average 72.9) mm, compared with 68-71.5 (average 69.3) mm in the lowland form macrurus. The ASI-Index is approximately 0.19. In all these highland subspecies is the larger size combined with differences in the colour-pattern from the low-

land form. Rand (1936b) adds Melidectes belfordi brassi as a recognizable mountain form, but it appears to be so similar to nominate belfordi that I do not accept it as a separate subspecies.

Other mountain species display size increase with rising elevation, but no differences in colour pattern between the populations. The most important ones are enumerated by Rand (1936b) and are here shown as the first five examples in Table 3. These species are restricted to the mountains, but nevertheless demonstrate larger wing-length with increasing height. Only Macropygia amboinensis is found down to the sea-level. In all these birds the differences between the populations are rather small and intergrading over large areas and have, therefore, not been regarded as great enough to justify a separation of populations as subspecies. The ASI-Indices vary between 0.08 and 0.63 which are comparatively small values.

In Table 3 has been added Paramythia montium which forms an especially interesting example, but was unknown when Rand wrote his paper. The large subspecies alpinum is distributed on the upper slopes of Oranje Mountains in Western New Guinea from 3.200 m to the tree limit about 4.100 m, while the smaller olivaceum ranges from 2.200 to 2.600 m in the Oranje, Nassau and Weyland Mountains. The altitudes mentioned in Table 3 are those at which the main material has been collected. The ASI-Index is large, 1.15. The wing-length of adult males of alpinum is 114-123 mm and of olivaceum 100-108 mm.

T a b l e 3. Wing-length (in millimeters) of populations of mountain birds in New Guinea, based on Rand(1936b), Paramythia on Salomonsen(1961)
n: number of specimens examined, altitude in m, average measurements in brackets

| Populations | Altitude | Wing-length | n | ASI-Index |
|------------------------------|----------|--------------------|---|-----------|
| Pachycephala schlegelii | 2.400 | ♂♂ 95-104 (100.4) | 5 | |
| Pachycephala schlegelii | 2.400 | ♀♀ 93-97 (95.3) | 4 | |
| Pachycephala schlegelii | 3.680 | ♂♂ 97-107 (101.4) | 5 | 0.08 |
| Pachycephala schlegelii | 3.680 | ♀♀ 101-102 (101.7) | 4 | 0.52 |
| Crateroscelis robusta | 2.000 | ♂♂ 61-64 (62.2) | 6 | |
| Crateroscelis robusta | 2,860 | ♂♂ 64-66 (65.3) | 4 | 0.58 |
| Poecilodryas sigilata | 2.400 | ♂♂ 92-93 (92.5) | 4 | |
| Poecilodryas sigilata | 2.400 | ♀♀ 89-92 (90.7) | 4 | |
| Poecilodryas sigilata | 3.680 | ♂♂ 100 (100.0) | 2 | 0.63 |
| Poecilodryas sigilata | 3.680 | ♀♀ 93-96 (94.3) | 3 | 0.31 |
| Macropygia amboinensis | 0 | ♂♂ 168-170 (169.0) | 2 | |
| Macropygia amboinensis | 1.250 | ♂♂ 171-174 (173.0) | 3 | 0.19 |
| Rallacula forbesi | 1.250 | ♂♂ 105-111 (108.0) | 2 | |
| Rallacula forbesi | 2.800 | ♂♂ 107-117 (114.2) | 6 | 0.37 |
| Paramythia montium olivaceum | 2.500 | ♂♂ 100-108 (103.7) | 8 | |
| Paramythia montium alpinum | 3.600 | ♂♂ 114-123 (116.8) | 7 | 1.15 |

There is also a difference in the colour pattern between the two forms. In the mountains of Central and Southeastern New Guinea nominate montium occurs up to the tree limit on 3.800 m, with a wing-length in adult males of 95-107 mm, and in the mountains of Huon Peninsula brevicauda up to an altitude of 3.600 m and with a wing-length in adult males of 100-105 mm (Salomonsen, 1961.). This means that only in the western mountains is a special high-mountain form (alpinum) developed with distinctly larger proportions than the population of the lower slopes. In all the remaining mountain ranges of New Guinea small forms of the same size as olivaceum occurs right up to the tree limit. It appears from the description above that the tree limit in these mountains is situated only a few hundred meters lower than in the mountains of western New Guinea.

The explanation of the difference between the size increase of the populations of the Oranje Mountains and those of the other mountains of New Guinea must have something to do with the fact that the western mountains are 500-800 m higher than the remaining mountains, reaching 4.884 m in the Carstenz Mountains. These highlands tower above the other mountain ranges of New Guinea and are capped with permanent snow and glaciers. Their ice-caps are remote and shrouded in cloud for much of the time. The western mountains are the only area in New Guinea with permanent ice on the peaks, and this fact together with the actual, considerable height and the great extension of the area lowers the ambient temperature very markedly, and in this way produce a so strong selection pressure that it has given rise to the development of the large alpinum. This form occupies the slopes downwards to 3.200 m altitude while the small forms elsewhere are found up to the tree limit on about 3.800 m. When the small form (olivaceum) in the western mountains occurs only up to 2.600 m it must be due to the fact that the superior size of alpinum radiates to the populations inhabiting lower altitudes through mixing of the gene-pools. The same phenomenon was described above for the central Asiatic highlands.

The case of Paramythia montium is not unique. Another example is Rhipidura albolimbata, of which the nominate form is found in all the mountain ranges in New Guinea in altitudes from about 1.500 m and upwards. In the Oranje and Nassau Mountains, however, it is replaced by lorenzi from 2.700 to 3.300 m, with a wing-length in adult males of 82-95 mm, compared with 75-82 mm in nominate albolimbata (Rand, 1942). When comparing the populations of Oranje Mountains it appears that adult males of nominate albolimbata at 1.800 m altitude has a wing-length of 81-82 (average 81.3) mm, and lorenzi at 2.800 m 82-89 (average 85.7) mm, giving an ASI-Index of 0.54. Another noteworthy case demonstrating a parallel development of a mountain form in the high parts of the Oranje Mountains is the genus Collocalia, described below. A similar zoogeographical status is found also in Melampitta lugubris lugubris and cacatua galerita triton, according to the measurements taken by Rand (1942). He finds the differences too small to give rise to separation of subspecies. The situation in Cacatua should be reconsidered, however; the ASI-Index is as large as 1.14.

Rand in his above-mentioned paper (1942) has demonstrated that in the Oranje Mountains no less than 40 species have increased size correlated with in-

creasing altitude. Even Rhipidura albolimbata shows very distinctly this increase taking place gradually in both lorenzi and nominate albolimbata. In other cases the size increase may be very modest, but nevertheless the tendency to larger size on higher elevations in the mountains is very convincingly demonstrated.

The same development as described above for the birds from Holarktis, Africa, Madagascar, Indonesia and New Guinea is also apparent in Southamerica. The birds of the upper slopes of the Andes are bigger than their lowland congeners. I may refer to the humming-bird genus Oreotrochilus of the Paramo zone of which the species are larger than virtually all lowland species of this family; cf. Nectarina tacazze and N.johnstoni in Africa. In many cases particular mountain subspecies have been developed, characterized not only by larger proportions but also by a colour pattern different from that of the lowland forms. In other cases there is a size increase with increasing altitude within the same subspecies, just as was described from New Guinea.

Traylor (1950:123) has made a thorough study of the altitudinal size variation in Bolivian birds, and his measurements are used for the preparation of Table 4. In all species mentioned a certain high altitude subspecies has been separated except in the two latter species (Suiriri and Vireo). The ASI-Indices do not differ from those of other tropical mountains described above. The index is particularly large in the Oven-bird Asthenes dorbignyi arequipae inhabiting the Puna zone.

T a b l e 4. Wing-length (in millimeters) of populations of mountain birds in Bolivia, based on Traylor(1950)

n: number of specimens examined, altitude in m, average measurements in brackets

| Populations | Altitude | Wing-length | n | ASI-Index |
|---------------------------------|----------|--------------------|---|-----------|
| Pitangus sulfuratus maximiliani | 400 | ♂♂ 115-122 (117.8) | 5 | |
| Pitangus sulfuratus maximiliani | 400 | ♀♀ 108-111 (109.5) | 2 | |
| Pitangus sulfuratus bolivianus | 2.750 | ♂♂ 129-133 (130.7) | 4 | 0.47 |
| Pitangus sulfuratus bolivianus | 2.750 | ♀♀ 125 | 1 | 0.60 |
| Asthenes dorbignyi dorbignyi | 2.500 | ♂♂ 61-66 (63.8) | 6 | |
| Asthenes dorbignyi dorbignyi | 2.500 | ♀♀ 62-68 (66.0) | 5 | |
| Asthenes dorbignyi arequipae | 3.900 | ♂♂ 74-79 (76.4) | 7 | 1.41 |
| Asthenes dorbignyi aerquipae | 3.900 | ♀♀ 71-74 (72.0) | 4 | 0.65 |
| Pyrrhura molinae restricta | 500 | ♂♂ 126-137 (131.5) | 2 | |
| Pyrrhura molinae molinae | 2.800 | ♂♂ 143-147 (145.0) | 2 | 0.45 |
| Suiriri suiriri | 500 | ♂♂ 69-74 (71.0) | 4 | |
| Suiriri suiriri | 500 | ♀♀ 70-74 (72.0) | 5 | |
| Suiriri suiriri | 2.500 | ♂♂ 75-81 (77.3) | 6 | 0.44 |
| Suiriri suiriri | 2.500 | ♀♀ 76-80 (77.7) | 3 | 0.40 |
| Vireo olivaceus chiri | 500 | ♂♂ 67-68 (67.5) | 2 | |
| Vireo olivaceus chiri | 2.700 | ♂♂ 70-77 (73.5) | 2 | 0.40 |

The variation in the Tyrant-flycatcher Suiriri suiriri is noteworthy. In the lowland of northern Argentina the range of measurement is 70-80 mm, which is intermediate between those of the Bolivian populations shown in Table 4. This shows that a U-shaped size cline runs from the southern lowland north to the tropical lowland (smaller size) and the Bolivian mountains (bigger size). In this way the size variation is similar to that of various Holarctic species, like Pica pica and Corvus corax, discussed above, in which a northern boreal form is replaced by a temperate southern population of smaller size and a mountain one of larger size.

Traylor (1950) makes an interesting comparison between the Bolivian and the New Guinea mountain birds (after Rand, 1936b). He arrives at the result that of a total of 42 mountain species in Bolivia 45% had increase in size with increasing altitude, 2% a decrease, while 53% showed no change in size. In New Guinea there were 69 mountain species, of which 33% had an increase in size, 1% a decrease, whereas 66% showed no change in size. These figures demonstrate a remarkable close agreement between the mountain avifauna in Bolivia and that in New Guinea. This accordance amply shows that the same response to altitude is developed in the two regions. A similar situation is undoubtedly to be found in all tropical mountains with stationary bird populations.

The size increase with increasing altitude is explained by almost all students as a result of the decreasing ambient temperature and is due to Bergmann's rule. I agree with this assumption which appears to be the only natural one. The bigger the body the better it is fitted to withstand cold, the smaller the body the more easily it can, through radiation and evaporation, lose heat. This must at least be the explanation for the size increase in species inhabiting the ground, bush or forests.

However, another factor that changes consistently with altitude must be taken into consideration. The air-pressure falls off by about 0.78% of sea-level pressure for every 100 m of altitude, and is not subject to important local variation, apart from a small effect by increasing humidity. The only student who has attributed the size increase in mountain birds to the fall in air-pressure is, so far I know, Moreau (1957) in his treatise of the African Zosterops. He adds, however, that "No conclusive evidence of such an effect appears to have been presented hitherto for any type of bird." His attempt to explain the correlation between size variation and decrease in air-pressure appears to be peculiarly complicated and affected, and on the next page (332) he appears to be of another opinion, stating that "Where populations otherwise similar are subjected to different minimum temperatures (and altitudes), those birds inhabiting the cooler climate have longer wings in 18 out of the 19 groups of comparable populations."

It is very improbable that the adaptive evolution in size in the mountain birds, described above, should be influenced by air-pressure. If it was the case it would signify that the aerodynamic efficiency of the wing was involved. It is hardly possible in these birds, living, foraging and breeding on the ground or in dense or open vegetation and not using the wings for more strenuous tasks. Savile (1957) has made a thorough study of the function and morphology of the avian wing and operates with various basic wing forms.

He calls the wing of passerine birds (with a few exceptions) and of various other birds "The Elliptical Wing" and states that at low and moderate speeds this wing plan is very efficient. He adds that "Wing-tip turbulence is slight, and pressure distribution is unusually uniform over the wing surface regardless of altitude." (216). In all probability this description must dispose of any influence of air-pressure on species with "elliptical wings".

On the other hand, birds which spend their whole life in the air (apart from the breeding time) must be extremely susceptible to the declining air-pressure, this particularly holding good of the Apodidae, and to a lesser degree also of the Hirundinidae, the Pseudochelidonidae and possible the Artamidae. The Swifts are by Savile (1957) said to have a "High-speed Wing". In another paper (Savile, 1950) he describes the flight mechanism of the Swifts and states that it does not alone include ordinary flight when they beat their wings in unison, but they also, during catching of prey, use beats of unequal strength in various manoeuvres, for instance stalling one wing in a short turn. This implies that the Swifts are highly dependable on the condition of the air, its turbulence, air-pressure, etc. It appears that the aerodynamic efficiency of the wings in both Swifts and Humming-birds involved a powered up-stroke, which is an appreciable factor in their speed of flight (Savile, 1950). It should be emphasized that Swifts living in mountainous areas are influenced by the decreasing temperature in the higher altitudes just like other birds, but that this influence is reinforced by that of the declining air-pressure.

In order to study this situation I have examined the species of Swiftlets inhabiting New Guinea, from where I could dispose over large series of specimens (Salomonsen, 1982). There are a number of species in New Guinea, of which Collocalia esculenta and C.spodiopygia both inhabit the country from sea-level to the tree-limit and are the subject of the following study. The species C.vanikorensis is not transgressing an upper limit of 1.400-1.600 m, but nevertheless displays a slight size variation with altitude. Finally, there are the large species within the superspecies C.orientalis, of which C.nuditarsus and C.orientalis (in Melanesia) appear to be mainly mountain birds, in this way supporting the hypothesis about the superior size of mountain birds. The third species of the superspecies, C.papuensis, is found right to the sea-level in New Guinea.

The measurements of Collocalia esculenta obtained in the western mountains of New Guinea (Oranje Range) are given in Table 5. The lowland subspecies (nitens) has a wing-length of 96-108 (average 100.8) mm and ranges upwards in the western mountains to about 800 m. The highland subspecies (erwini) has a winglength of 107-120 (average 113.1) mm, an appreciable size increase. This subspecies is found in the areas above 1.600 m, which altitude in New Guinea signifies the general change from a tropical lowland environment to a subtropical and montane one. Cf. also what is said above on the same change in Zaire.

The size of C.esculenta increases gradually when moving upwards in the mountains, and the zone between the areas of nitens and erwini are inhabited by populations intermediate in size; are here called erwini \approx nitens. The ASI-Index, calculated in all populations with the lowland population as

T a b l e 5. Wing-length (in millimeters) of populations of Collocalia esculenta in the Western Mountains (Oranje Range) in New Guinea, after Salomonsen(1982)

n: number of specimens examined, altitude in m, average measurements in brackets

| Altitude | Wing-length | n | ASI-Index |
|--------------------|-----------------|----|-----------|
| 0-800, average 400 | 96-108 (100.8) | 46 | |
| 1.200 | 107-110 (108.5) | 4 | 0.96 |
| 2.200 | 107-118 (113.0) | 4 | 0.67 |
| 2.800 | 113-118 (114.3) | 4 | 0.59 |
| 3.200 | 108-115 (111.5) | 6 | 0.38 |
| 3.600 | 112-120 (116.0) | 2 | 0.47 |

basis, is rather high, 0.4-1.0. It is not higher, however, than in the birds enumerated in Table 1-4 with "elliptical wings" which were dependent only on the decreasing air-temperature and not on changes in air-pressure. The Swiftlets, which are influenced by a combination of the two factors should be supposed to have a larger ASI-Index than the other birds. It is possible, however, that temperature conditions are of only minor importance for the Swiftlets, because they are independent of the microclimatical temperature oscillations of the ground and low vegetation, as they frequent only the upper air-masses.

The size variation of Collocalia esculenta in various mountain areas of New Guinea is shown in Fig. 1. The situation in the Western mountains has been described above and appears from Table 5. In the other New Guinea mountains the size variation differs distinctly from that in the Western mountains. In the Central mountains, including the Kubor Range, Bismarck Range, Hindenburg Mountains and surrounding mountains, the body proportions of esculenta are smaller and the limit towards the size of erwini is just skirted. In the Eastern mountains (including Wharton Range and Surroundings) erwini does not occur at all, even not at the highest altitudes investigated (3.680 m), where the intermediate form erwini \approx nitens is found (average wing-length 106.3mm). According to the rather meagre material from Southeastern New Guinea (from Hall Sound to Owen Stanley Range) these areas are inhabited by the lowland form nitens, with a wing-length not exceeding 100 mm even at 2.200 m altitude. The peripheral mountains of New Guinea from where material has been examined, including Arfak Mts., Weyland Mts., Wissel Lake area, Sepik Mts., Saruwaged Mts. and Huon Peninsula Mts., are inhabited by nitens or the intermediary erwini \approx nitens, with wing-lengths varying between 101 and 109 mm (Salomonsen, 1982).

It appears from what have been said about Collocalia esculenta and from Fig. 1, that the size variation of this species in the New Guinea mountains follows exactly the same pattern as described above for Paramythia montium, Rhipidura albolimbata and other species, demonstrating that only in the Western mountains is the selection pressure so strong that it has given rise to the development of mountain forms with large proportions.

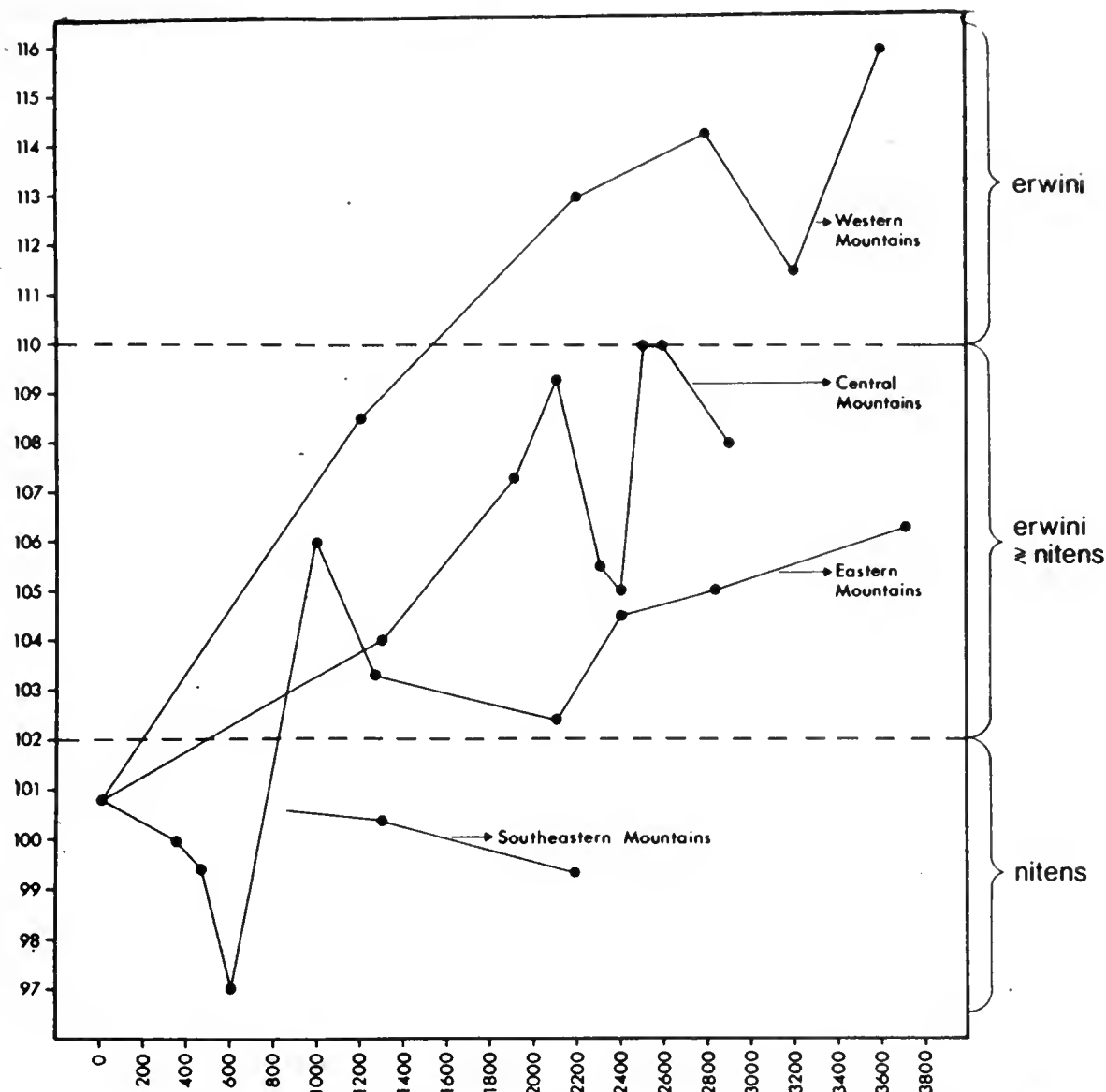


Fig. 1. Average wing-length (in millimeters) of Collocalia esculenta populations in New Guinea (ordinate) in relation to altitude (in meters) of various mountain ranges (abscissa). The subspecific categories are mentioned to the right

The altitudinal variation in New Guinea of the wing-length in Collocalia spodiopygia is an exact counterpart to that in C. esculenta. The difference between the lowland and the highland form is even larger in spodiopygia than in esculenta. The lowland form (hirundinacea) has a wing-length of 114-117 (average 115.6) mm and is found up to an altitude of about 1.500 m. The highland form (excelsa) has in the Western mountains (Oranje Range) a wing-length of 120-137 (average 127.7) mm. The extraordinary large size of excelsa appears from the diagram Fig. 2, which shows the wing-length of all subspecies within spodiopygia, after measurements taken by Salomonsen (1982). It is distinctly to be seen that excelsa is larger than all other subspecies of spodiopygia. This was to be expected, because excelsa is the only form of spodiopygia in which the size increase is a response to environmental influences. However, the considerable spreading of the measurements in excelsa, from 120 to 137 mm, is not a natural phenomenon, but is due to the fact that all populations have been gathered in this collective measurement, in spite of the fact that the size of the populations gradually increase with increasing altitude. The measurements of the single populations are given in Table 6. It appears from this table that the population inhabiting 1.600 m altitude is intermediate between the two forms (excelsa \approx hirundinacea) and that the average wing-length increases from 122.9 mm on 2.200 m altitude to 131.9 mm on 3.800 m. The ASI-Indices vary from 0.24 to 0.47, slightly smaller than those of esculenta shown in Table 5.

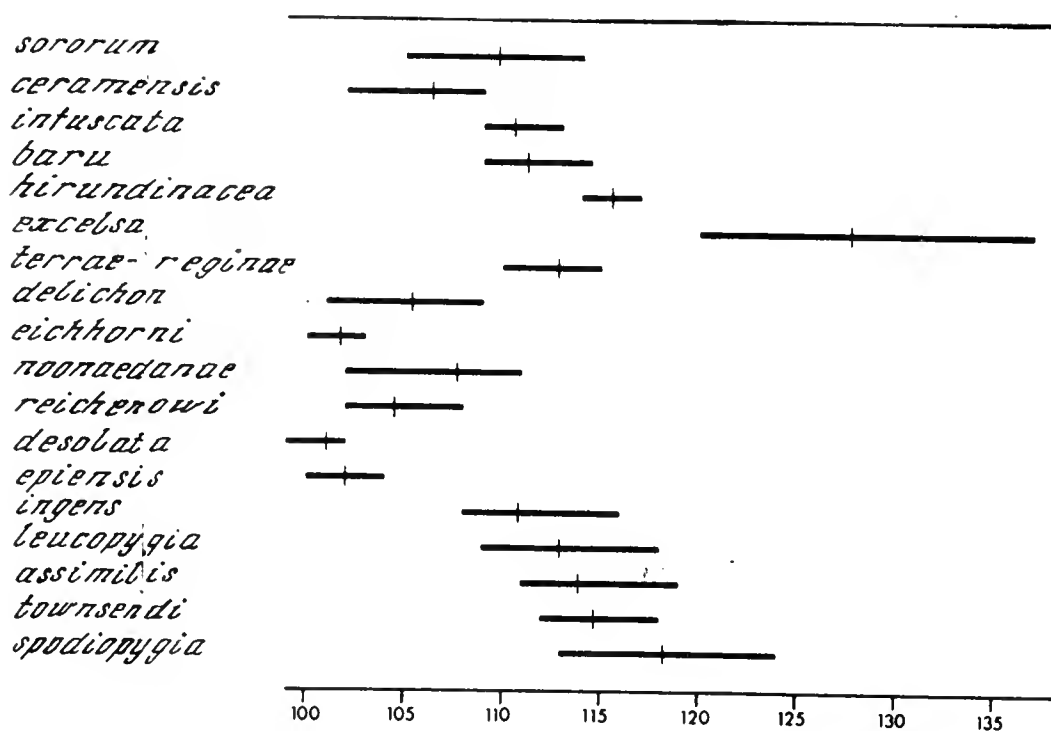


Fig. 2. The variation in wing-length (in millimeters) of all subspecies of Collocalia spodiopygia, ♂♂ and ♀♀ combined. The average values are shown by vertical marks

Just as in C.esculenta the highland form of spodiopygia is found only in the Western mountains, while the wing-length is much smaller in the other mountain areas of New Guinea. The material is, however, much more scarce than in esculenta. Some specimens from the Schrader Range in the Central mountains at 2.250 to 2.650 m altitude have wing-measurements of 113-116 mm, which are not bigger than those of the lowland form hirundinacea. A long series from Wharton Range, in the Eastern mountains, from sea-level to 3.680 m, has a wing-length of 113-125 (average 117.1) mm which is very similar to the wing-length of those specimens collected at 1.600 m in the Western mountains. The measurements just skirt the lower limit of the size of excelsa, and the birds in question must be said to belong to the intermediate form excelsa \geq hirundinacea.

All evidence points to the conclusion that the size variation of spodiopygia in the New Guinea mountains forms an exact parallel to that of esculenta, both in size increase, geographical distribution and altitudinal adaptation. The explanation of the evolution of a special highland form in the Western mountains, must therefore be the same as that given for Collocalia esculenta, Paramythia montium and other birds mentioned above.

Table 6. Wing-length (in millimeters) of populations of Collocalia spodiopygia in the Western Mountains (Oranje Range) in New Guinea, based on Rand (1942) and Salomonsen(1982)

n: number of specimens examined, altitude in m, average measurements in brackets

| Altitude | Wing-length | n | ASI-Index |
|----------------------|-----------------|----------------|-----------|
| 0-1.600, average 800 | 114-117 (115.6) | (Large series) | |
| 1.600 | 113-122 (117.8) | 9 | 0.24 |
| 2.200 | 120-127 (122.9) | 6 | 0.45 |
| 3.225 | 121-130 (125.0) | 11 | 0.34 |
| 3.800 | 125-137 (131.9) | 14 | 0.47 |

The third species of Collocalia in New Guinea, C.vanikorensis (in the form granti) has the upper limit of its range at about 1.500 m. Owing to its attachment to lowland it has not been able to develop high-mountain forms such as do C.esculenta and C.spodiopygia. Nevertheless, vanikorensis demonstrates a distinct tendency to increase the wing-length with altitude. In a series of specimens of Southeast New Guinea those from below 100 m altitude measured 113-117 (average 115.5) mm, and those from 1.250 m 118-123 (average 120.0)mm. The ASI-Index is 0.25. This difference in wing-length is interesting since it shows that the correlation between body proportions and altitude is discernible even in comparatively low mountain ranges, and that the same extreme susceptibility to the altitudinal environmental factors is found in all the said three species of Collocalia in New Guinea.

Still more noteworthy is the fact that the still lower mountains in New Ireland, in the Bismarck Archipelago, has a similar influence on the size of C.vanikorensis. A large series (67 specimens) of the lowland population in New Ireland (the subspecies pallens) measure 113-124 (average 117.7) mm, whereas 3 specimens from the Lelet Plateau in about 900 m altitude had a wing-length of 117-125 (average 122.3) mm. The ASI-Index is 0.43, which is rather high.

The same altitudinal variation holds good of C.spodiopygia (the subspecies noonaedanae). A series of 30 specimens from about sea-level had a wing-length of 101-109 (average 104.7) mm, 9 specimens from Lelet Plateau 102-111 (average 106.1) mm; ASI-Index 0.15. Collocalia esculenta, on the other hand, does not show any size variation with altitude in the Bismarck Islands; cf. Salomonsen 1982 for closer information about these birds.

The fact that C.spodiopygia and C.vanikorensis in the New Ireland mountains in a modest scale has developed an adaptation to the environmental factors of the higher altitudes, demonstrates the large susceptibility of the Swiftlets to the influence of the variability of the air-pressure. It must be due to the dependence of air-pressure in Swiftlets that the development of greater size in the upper parts of the New Ireland mountains has taken place. It can be added that among the many species with "elliptical wings" which were collected in the Lelet Plateau not a single one showed any increase in size in the mountains.

The correlation between increase in wing-length and increase in altitude, which is so distinct in the Collocalia species of New Guinea, must not invite to the belief that the Swiftlets are stationary birds. Their extraordinary capacity of flight, the fact that they spend almost their whole life in the air, makes it an easy matter for them to follow air-currents vertically or in other ways change their altitudinal position. Each population must have a certain altitudinal amplitude, and if I were to venture an opinion I would estimate a maximum of about 500 m. On the other hand, the agreement between body proportions and altitude demonstrates obviously that local populations have developed a certain adaptation to the environmental conditions in the particular altitude. If imagining that all populations mixed in the mountains all morphological differences would be swamped, because gene-pools of individuals of various types would be completely mingled, and there would be no possibility for developing altitudinal populations with

different morphology. Another question is why populations keep within certain altitudinal air-masses and do not transgress these limits. Nothing is known about such phenomena in birds, but intense studies in human physiology have demonstrated that retinal hemorrhage and pulmonary edema are the most conspicuous physiological responses during longer sojourns of human beings in high altitudes (Houston, 1980). If a similar physiological situation is present in Swiftlets it is understandable that they keep within certain limits of the air-masses to which they are adapted.

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THE INFLUENCE OF ICE ON THE ECOLOGY OF ARCTIC AND ANTARCTIC SEABIRDS

R.G.B. Brown

Seabird Research Unit, Canadian Wildlife Service, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada

Ice is the dominant feature of polar environments. The terrestrial ice caps of Antarctica and the Arctic are surrounded by even greater areas of ice on the sea, and these have profound effects on the world's climate at great distances from the poles. The outflow of ice and cold water from the Arctic Ocean and Baffin Bay, for example, extends the southern boundary of the Arctic as far south as 46°N off eastern Canada, while the countervailing, warm North Atlantic Drift on the European side of the Atlantic takes it as far north as 71°N (Salomonsen, 1972). In one way or another the ecology of very many species of birds in both hemispheres is influenced by these polar ice masses. The object of this paper is to summarise the various effects which ice on the sea has on seabirds, with particular emphasis on conditions in the Canadian Arctic.

The most important source of ice on the sea comes from the freezing of the sea itself. The pack-ice thus formed covers some 20 million km^2 of the sea around Antarctica, and over 10 million km^2 in the northern hemisphere, mainly in the Arctic Ocean (Bridinger, 1981). Arctic Ocean ice drifts into the Atlantic with the East Greenland Current, and to a lesser extent with the Labrador Current, and its winter maximum extends, respectively, to southwest Greenland and northern Newfoundland. These limits mark the southern boundary of Salomonsen's (1972) Low Arctic zone of the marine environment. The High Arctic zone, set by the southern boundary of pack-ice in summer, extends to southeast Greenland and southern Baffin Bay in the western Atlantic. The zonal limits in the Pacific sector are, respectively, the Aleutians and Bering Strait. Pack-ice is distributed fairly evenly around Antarctica, extending to $c.60^{\circ}\text{S}$, but a little farther north in the South Atlantic.

The other sources of ice are icebergs. These are very large pieces of freshwater ice, formed by the compacting of snow falling on the terrestrial ice caps, and entering the sea at the tips of glaciers (Budinger, 1981). Almost all Arctic icebergs come from fjords in west Greenland, and they are virtually confined to Baffin Bay and eastern Canadian waters south to $c.41^{\circ}\text{N}$. Most Antarctic icebergs, by contrast, calve off broad ice shelves, mainly in the Ross and Weddell Seas, and they are very large - up to 333 km long, against only 11 km for the largest Arctic berg. They are fairly evenly distributed over the waters around Antarctica.

Ice on the sea enhances the marine biological environment at many levels. There is, for example, evidence that water in glacier fjords contain high levels of nitrates and silicates, the nutrients required for the growth of phytoplankton (Dunbar, 1951; Apollonio, 1973). These are probably brought up from the bottom by upwelling, caused by the flowing of melt water away from the glacier face. Upwelling of this kind also occurs along the sides of both Arctic and Antarctic icebergs, with water being brought to the surface from as deep as 200 m, though it is not known whether this also brings up significant quantities of nutrients (Neshyba, 1977; Petersen, 1977). Winds blowing

parallel to the edges of extensive stretches of pack-ice will also induce upwelling (Buckley et al., 1979). Studies reviewed by Dunbar (1981) have demonstrated an enhanced phytoplankton bloom in a zone which may extend as much as 50 km from an ice edge, but it is not clear whether this is the result of nutrients brought by such upwelling into the euphotic zone, or whether it follows from the release of algae into the water as the ice melts.

Recent investigations have shown that the underside of pack-ice supports a distinctive community of plankton and fish (reviewed by Dunbar, 1981; see also Bradstreet, Cross, 1982; Cross, 1982). The bases for this epontic community are diatoms in the bottom few centimetres of the ice floes. The growth of this flora begins in late winter or early spring, well before the start of the phytoplankton bloom in the water column, and Dunbar (1981) suggests that it may make up as much as a quarter of the total primary production in the Arctic Ocean. (The contribution to Antarctic production is probably less, because of the higher overall productivity in those waters.) Bradstreet and Cross (1982) point out that the early start of this production means that the herbivorous zooplankton, at the next trophic level in the food web, have an annual grazing season of as much as four months, against only two months in Arctic waters where there is no ice and they can rely only on the phytoplankton in the water column.

The community of epontic invertebrates, mainly made up of amphipods, copepods and other crustaceans, is broadly similar in both Arctic and Antarctic pack-ice (Dunbar, 1981). At the next trophic level there are fishes; three species of notothenids Trematomus spp. occur in Antarctic ice and in the Arctic there are two gadoids, Boreogadus saida and Arctogadus glacialis. But while Trematomus only occurs as fry and fingerlings, Boreogadus and Arctogadus are of all ages. As an indication of their enormous abundance in Arctic pack-ice, Bradstreet (1980) has estimated that Uria lomvia alone took some 1.5 million of these fish during a 35-day period in early summer at the ice edge in Lancaster Sound. They are, in fact, central to the food-web in the Canadian High Arctic. The energy from the epontic primary production is channelled through herbivorous crustaceans, both epontic and free-swimming, to Boreogadus, and from there on up to seabirds - Fulmarus glacialis, Rissa tridactyla, Uria lomvia and Cepphus grylle - as well as to whales and seals (Dunbar, 1981; Bradstreet, Gross, 1982). The only important seabird in Canadian High Arctic waters which does not depend directly on Boreogadus for its food is Alle alle, which instead feeds mainly on free-swimming amphipods and copepods under the ice (Bradstreet, 1982).

More generally, seabirds make extensive use of pack-ice, both in the Arctic and Antarctic. In the Arctic the species most closely associated with ice are Fulmarus glacialis, Pagophila eburnea, Rhodostethia rosea, Uria lomvia, Alle alle and Cepphus grylle (Divoky, 1979; Renaud, Bradstreet, 1980; McLaren, 1982; Renaud et al., 1982). The equivalent list for the Antarctic includes Aptenodytes forsteri, Pygoscelis adeliae, Thalassoica antarctica, Pagodroma nivea, Oceanites oceanicus and Sterna paradisaea (Routh, 1949; Holgersen, 1957; Cline et al., 1969; Ainley, Jacobs, 1981). At both poles the dominant species are almost all birds which feed either by pursuing prey underwater, or picking it at the surface (Ashmole, 1971). Densities are variable, but locally they can be very high. Ainley and Jacobs (1981) found bio-

masses of over 200 kg/km^2 in the Ross Sea in summer, and Divoky (1979) of over 500 kg/km^2 in the south east Bering Sea in winter. Divoky reported flocks of up to 25,000 Uria spp. at the Bering Sea ice edge, and Renaud et al. (1982) estimated that at least 14 million Alle alle occurred near the ice edge in northwest Baffin Bay in spring. Investigation of these seabird communities has only just begun, however, and some interesting questions need to be answered. Why, for example, are the seabird communities in the Chukchi and Bellingshausen Seas apparently poorer than those at other ice edges in, respectively, the Arctic and Antarctic? And why is there no small, plankton-feeding diver equivalent to Alle alle in the Antarctic and in the Pacific sector of the Arctic, despite the occurrence, respectively, of Pelecanoides spp. and Aethia spp. at lower latitudes?

Seabirds are also attracted to glacier faces and to icebergs. The upwellings at glacier faces not only bring up nutrients to enrich production in the long term; they also bring up prey and concentrate it there at densities high enough for economical foraging (Brown, 1980a). One such glacier face in Spitsbergen attracted large numbers of seabirds, especially Fulmarus glacialis, Sterna paradisaea and Rissa tridactyla - the lastnamed species travelling at least 50 km to feed there (Hartley, Fisher, 1936; Stott, 1936). The food in question was large swarms of the euphausiid Thysanoessa inermis. Similarly, flocks of Phalacrocorax atriceps and Sterna hirundinacea were attracted to a Chilean glacier (Brown et al., 1975). More generally, surveys of north west Baffin Bay have shown that Fulmarus glacialis, Rissa tridactyla and Pagophila eburnea were commoner along glaciated stretches of coastline than along unglaciated stretches (McLaren, Renaud, 1982; Renaud, McLaren, 1982).

The grinding together of pack-ice in motion inevitably leads to the crushing of organisms in the water between the floes, and Pagodroma nivea, a species strongly associated with the Antarctic pack-ice, may get much of its food in this way (Falla, 1964; Cline et al., 1969). When icebergs drift through the pack they often overturn floes, and this allows seabirds to feed on the exposed epontic organisms. It is not known how significant this is in providing food under natural conditions, but it is commonplace in the Arctic to see Rissa tridactyla, and to a lesser extent Sterna paradisaea, feeding on Boreogadus exposed in this way by icebreaking ships (Andriashev, 1970).

The mere physical presence of ice assists foraging seabirds in other ways. Pack-ice damps down waves and spray, and this presumably helps foraging in stormy weather. Many seabirds use both pack-ice and icebergs as resting places. In the Arctic this is especially true of Pagophila eburnea (Salomonsen, 1972; but see also Brown et al., 1974). Flocks of Rissa tridactyla often rest on Arctic icebergs (R.G.B. Brown, unpublished observations), and several species do so in the Antarctic (Routh, 1949). Of the latter, Pachyptila spp. and Halobaena caerulea also use the water immediately surrounding the berg as a feeding area. Others, such as Thalassoica antarctica, Pagodroma nivea and Pygoscelis adeliae, instead use the iceberg as a floating base from which they can sally out to forage in waters some distance away. Such behaviour presumably reduces the energetic costs of foraging, and by resting on

the ice rather than on the water the birds avoid the risk of having water freeze on their feathers, or of frostbite to their legs and feet (Madsen, Wingstrand, 1959; Salomonsen, 1972).

Finally, the presence of pack-ice has an important influence on the timing and routes of the migration of seabirds and waterfowl in the spring, partly because most seabirds avoid very dense pack-ice (Cline et al., 1969), but also because the birds can feed along the ice edge while they are on passage, or wait there until the land is sufficiently free of snow for them to be able to start to nest (Prach et al., 1981). Indeed, in the very long term, ice edges may have determined the migratory patterns of whole populations of seabirds. Salomonsen (1972) has suggested that the two major migratory paths followed by High Arctic alcids in the North Atlantic - Uria lomvia and Alle alle from the European Arctic travelling to winter quarters off west Greenland, and those from Baffin Bay going to Newfoundland - were originally determined by the positions of the edges of the Arctic ice cap at the end of the last glaciation.

Under certain circumstances the absence of ice in otherwise frozen seas can be just as important as its presence, especially if this open water recurs year after year. Such areas are called "polynyas" if they are non-linear in shape, and "leads" if they are linear (Pilot..., 1970). One can make a further distinction between primary polynyas which remain open all winter, and secondary ones which freeze over but which become ice-free early in the spring. The most important factor in keeping these areas ice-free is the wind, which drifts the ice away as fast as it is formed in polynyas; or rotates the pack-ice and thus causes fracture lines which open into leads (Dunbar, 1981; Smith, Rigby, 1981). In shallow waters the action of tides and currents is important in keeping the smaller polynyas open, and melt water from ice caps and snow banks on land will also create small openings in otherwise dense, landfast ice (Smith, Rigby, 1981, D.N. Nettleship, pers. comm.).

The distributions of recurring polynyas is best known for the Canadian Arctic (Smith, Rigby, 1981). The largest is the North Water polynya in northern Baffin Bay, but there are also significant areas of open water in winter in eastern Lancaster Sound, north west Hudson Bay, off south east Baffin Island and in the southeastern Beaufort Sea. The sea is also kept open all winter up to c. 70°N along the west coast of Greenland, by relatively warm water originating in the North Atlantic Drift (Oceanographic..., 1958). It's not a true polynya as it is not completely enclosed in ice but opens at the south into the Labrador Sea but, because of its biological importance, it will be included in this discussion.

The obvious advantage of a polynya is that it allows seabirds access to feeding areas which would otherwise be closed to them if the sea was frozen over. Presumably the attraction is to the epontic community at the ice edge, rather than to open water as such. But to what extent do seabirds actually make use of polynyas in winter? Not very much information is available, because of the inaccessibility of polynyas in winter, and also because of the darkness at that season. However, it appears that few birds winter in the High Arctic polynyas such as the North Water; only Cephus grylle appears to

do so, in small numbers (Renaud, Bradstreet, 1980; Brown, Nettleship, 1981). The only other seabird to winter so far north is Rhodostethia rosea, whose whole population apparently winters in leads and polynyas in the Arctic Ocean (Collett, Nansen, 1900; Divoky, 1979).

In contrast, the polynyas and leads in the Low Arctic, in Hudson Strait and Bay, are very extensively used. Cephus grylle and Somateria mollissima are the commonest species, but Uria lomvia, Alle alle and Larus hyperboreus also occur there (Brown, Nettleship, 1981; Prach et al., 1981). The "polynya" along the west Greenland coast is even more important; Uria lomvia, Alle alle, Cephus grylle, Phalacrocorax carbo, Larus marinus, L.(g)glaucoides and L.hyperboreus all winter there (Salomonsen, 1951, 1967). Many of these are local birds, but banding returns have shown that most of the Uria lomvia, for example, come from Spitsbergen, Novaya Zemlya and, to a lesser extent, from the Canadian High Arctic (Salomonsen, 1967, 1971; Gaston, 1980). The greater importance of this "polynya", in comparison with the true polynyas farther north and west, probably stems from its larger size and marginally milder climate, and to the fact that birds from the European Arctic have access to it via the Labrador Sea.

In summer, recurring polynyas and the leads associated with them have a decisive influence on the siting of seabird colonies in both the Arctic and the Antarctic. Stonehouse (1967) noted the coincidence of polynyas with colonies of Aptenodytes forsteri and Pygoscelis adeliae in the Ross Sea. Brown and Nettleship (1981) knew of only one major seabird colony in the Canadian Arctic (a poorly-known colony of Cephus grylle in Jones Sound) which was apparently not beside a polynya. This does not mean that every polynya has a seabird colony beside it, because in many cases the nesting habitat is unsuitable. Nonetheless the coincidence between colonies and polynyas is a very striking one. All major Alle alle colonies are beside primary or secondary recurring polynyas, or other open-water areas which never freeze (Brown, 1980b). The only colony of Uria lomvia in the western Canadian Arctic, at Cape Parry, is beside the only major polynya in the Beaufort Sea (Brown, Nettleship, 1981). The abundance of seabirds along the open west coasts of Greenland and Novaya Zemlya is in sharp contrast to their scarcity along the ice-bound east coasts (Uspenski, 1958; Salomonsen, 1979; Oceanographic..., 1958).

One reason for this association is the greater availability of food in a polynya. The birds have access to the epontic community at the edge of the polynya as soon as they arrive in spring (Bradstreet, Cross, 1982). But there will also be significant advantages later in the summer after the ice has gone. Pavshchik (1968) found that the zooplankton bloom in Davis Strait occurred in July in the west Greenland "polynya", in August in the middle of the Strait, but not until September along the Baffin Island coast where the ice persists longest. The effect of this is to provide an early supply of food by the time the young seabirds begin to hatch from late July onwards (Salomonsen, 1951; Gaston, Nettleship, 1981). This allows the birds 4-6 weeks in which to raise their young and leave the colony before the Arctic summer ends at the beginning of September. It is unlikely that they could do so in areas where persistent ice cover delayed the bloom until August or September.

The second advantage of breeding close to a polynya is that it allows the birds early access to the colony site in the spring. This, again, is important

in the short Arctic summer. The more specialised cliff-nesting species are the ones which are most affected. All the Uria lomvia colonies in west Greenland and the Canadian Arctic are close to areas of open water in spring (Brown, Nettleship, 1981: Fig. 1). So are those of Fulmarus glacialis, but in addition this species breeds at sites in eastern Baffin Island accessible in spring only by crossing unconsolidated pack-ice. Neither species breeds on the central east coast of Baffin Island where landfast ice persists all summer. Instead, Larus hyperboreus and related species breeds in many small colonies beside the very small polynyas along' that part of the coast (D.N. Nettleship, pers. comm.) (The same relationship between these species holds good for east Greenland too; compare Salomonsen (1979: Figs. 1, 3) with ice maps in Oceanographic... (1958). Brown and Nettleship interpreted these differences in terms of the species' differing flight abilities. Uria needs a 8-10 m "runway" to take off from the water, and probably cannot take off from ice at all (Freuchen, Salomonsen, 1958; Uspenski, 1958), and is thus at risk when it crosses wide expanses of pack-ice. Fulmarus is only a little more agile. But Larus is an agile flyer, well able to take off from flat surfaces or small patches of open water, and it is presumably this ability which has allowed it to exploit the small polynyas inaccessible to the more specialised cliff-nesting seabirds.

More generally, one can put the importance of polynyas to seabirds into perspective by seeing what happens when for some reason a recurring polynya fails to form. Kartashev (1960) and Salomonsen (1951) described partial or total breeding failures of, respectively, Uria lomvia and Alle alle under such circumstances, and Barry (1968) reported a massive mortality of sea ducks in a spring when the principal polynya in the Beaufort Sea failed to open up. But the most striking example occurred in 1978, when the normal spring extension of the North Water polynya into Lancaster Sound failed to develop (Nettleship et al., 1980). The result was a disastrous season for the seabirds breeding deep in the Sound on Prince Leopold Island (Gaston, Nettleship, 1981). Few of the surface-feeding species (Fulmarus glacialis, Rissa tridactyla, Larus hyperboreus) attempted to breed. Most of the diving species (Uria lomvia, Cephus grylle) did so but, for lack of food, only a few of them raised young; the young Uria which did survive suffered further heavy mortality from predation by Larus hyperboreus, which took the flightless chicks as they tried to cross the pack-ice to reach open water.

In summary, it is clear that ice on the sea influences the ecology of both Arctic and Antarctic seabirds at many levels, from short- and long-term enrichment of local feeding conditions, to the determination of their breeding and winter distributions, and even their migration routes. But it is also clear that the investigation of these effects has barely begun. There is as yet no survey of the distribution of polynyas in Antarctica or the Eurasian Arctic. Given modern satellite imagery this would be an easy thing to do, and it is basic to our understanding of the summer and winter ecology of the seabirds of those regions. We need to know much more about the timing of the annual cycles of plankton production both in polynyas and in the adjacent ice-covered waters. Again, why should ice edges in the Ross Sea and the North Water support so many more seabirds, and species of seabirds, than those, say,

in the Bellingshausen and Chukchi Seas? These are only a few of the questions which need answering. But it is encouraging to see the great advances which have been made in research on ice, ice biota, and the importance of both to seabirds and other large predators, all within the last ten years. Let us hope that this trend continues.

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POLYCYCLICITY AND HYPOMORPHIC EFFECT IN REPRODUCTION
OF MOUNTAIN BIRDS

A.F.Kovshar

Institute of Zoology of the Kazakh SSR Academy of Sciences, Alma-Ata, USSR

The fecundity of birds populating mountain ridges has been attracting the attention of Soviet ornithologists over 20 years. Stepanyan (1959) was the first to suggest that limited food resources for some insectivorous birds determined a lesser, as compared with the plain populations of these species, intensity of reproduction in the alpine zone which is expressed both in the decrease of the egg number in clutches and in the presence of only one egg laying per season. Later this phenomenon was called hypsomorphic effect (Stepanyan, 1970).

This problem was then discussed in a number of papers on Caucasian and Middle-Asian species (Ivanov, Chunikhin, 1961; Chunikhin, 1962; Potapov, 1966; Kovshar, 1966, 1971; Böhme, 1968). The results proved to be contradictory: some authors recognized the presence of hypsomorphic effect, whereas others rejected it.

Our observations of 1959-1967 in Western Tian-Shan (the Talassky Alatau Ridge) and 1967-1978 in Northern Tian-Shan (the Zailiisky Alatau) at heights of 2,400-3,000 m above the sea level allowed us to consider this problem using a new material of higher quality. Analysis of the data from over 3 thousand nests of 58 species of the Passeriformes confirmed the general tendency to a decrease in the clutch size in a number of species of widespread insectivorous birds represented in the mountains by special subspecies. E.g., in Anthus trivialis trivialis L. the size of a clutch is 4.7-4.8 eggs per nest in the European part of the USSR, whereas in A.t.harringtoni Witherby it is 4.2 in the Tian-Shan; in Turdus merula merula it is 4.6-4.8 in the plain, and in T.m.intermedia Richm. 4.2 in the mountains; in Phylloscopus inornatus inornatus Blyth it is 6.0 in Transbaikalia and Yakutia and in Ph.i.humei Brooks 4.8 in the mountains, etc. A distinct decrease of the mean indices of the clutch size was also noted in Turdus viscivorus bonapartie Cabanis, Phylloscopus trochiloides Sund., T.troglodytes tianschanicus Sharpe, Parus ater rufipectus Sev., and some other species. A decrease of the upper limit of the clutch size is also demonstrative in the mountain subspecies: in A.trivialis, T.viscivorus and Phyl.inornatus by one egg; in T.merula, T.troglodytes and P.ater by two eggs, and in Parus songarus Sev., as compared with closely related species P.montanus L. (situation "species-subspecies"), even by three eggs.

As was already mentioned in my previous paper (Kovshar, 1971), the differences between the Tian-Shan and the forest zone could be due not only to the absolute height but also to the geographical latitude directly related to the length of daylight. Special observations carried out in 1976-1978 simultaneously in two localities of the same canyon in the Zailiisky Alatau at heights of 1,500 and 2,500 m above sea level (practically at the lower and upper boundaries of the coniferous forest zone) have shown that the clutch size in a number of species (Ph.inornatus, Ph.trochiloides, P.ater, etc.) is not so much influenced by the absolute height as by the geographical latitude. In other words, potential fecundity of insectivorous birds depends not only

on food abundance at a certain absolute height, but also on the possibility of its obtaining related to the length of daylight.

The second component of the hypsomorphic effect, monocyclity of reproduction, is not confirmed by our observations. The first documentary evidence of two reproductive cycles in song birds in the Tian-Shan was obtained in collaboration with E.I.Gavrilov and E.F.Rodionov at the end of the sixties when two clutches per season were found in T.troglodytes, Calliope pectoralis ballionix Sev., Motacilla personata Gould., M.cinerella caspica Gm. (Gavrilov, Kovshar, 1968; Rodionov, 1968).

In the course of observations over individually marked birds in 1971-1978 over 50 reliable cases of two reproductive cycles were registered in 10 avian species: M.personata, M.cinerea, Phoenicurus erythronotus Sev., Phoenicurus coeruleocephalus Vig., Prunella fulvescens fulvescens Sev., P.atrogularis hut-toni Moore, T.troglodytes tianshanicus Sharpe, Ph.inornatus humei Brooks, Mycerobas carnipes mersbacheri Schal. Double nesting during the season is a normal phenomenon for 9 out of 10 listed species, and solely in Ph.inornatus the second clutch appears to be observed only during the most favourable years. On the other hand, in two species (P.fulvescens and Ph.erythronotus) even triple nesting during the season was registered, and in P.fulvescens four clutches were observed two years running; out of these clutches the third one perished and all the others were successful (Kovshar, 1975). These facts alter markedly our ideas on the possibilities of reproduction of insectivorous birds in the subalpine zone.

There is every reason to believe that two reproductive cycles are characteristic not only of those 10 species for which they were confirmed. For example, T.viscivorus, T.merula and Carduelis paropanisi Koll. in the Zailiisky Alatau have, undoubtedly, two clutches as evidenced by the two-peaked curve of their breeding season in which the distance between the peaks exceeds the duration of the nest period in these species. Eight other species have, very likely, the second clutch: Anthus spinoletta blaistoni Swinh., A.trivialis harringtoni Witherby, Phoenicurus erythrogaster grandis Gould., Saxicola torquata maura Pall., Oenanthe oenanthe L., Laiscopus himalayana Blyth, L.collaris rufilata Sev., Serinus pusillus Pall. The second clutch is not excluded even for Loxia curvirostra tianschanica Laumb. which nested in 1974 in July-August and in December (the interval between these nestings is sufficient for the feeding of the young).

The percentage of birds taking part in the second nesting depends on the specific characteristics of the year, the success of the first reproductive cycle, and on some other reasons. The annual fluctuations can be so significant that the same species, depending on the year conditions, can be either monocyclic, or dicyclic. For example, in the Zailiisky Alatau A.trivialis harringtoni had one clutch in 1971-1974 and two in 1975-1976.

During polycyclic reproduction under conditions of a short summer time is being saved as the result of: a) shorter preparation for nesting and b) partial overlapping of the successive reproductive cycle phases. If in spring the place for the nest is sometimes being chosen during several weeks, in summer it is chosen during a few days. The nest construction during late nesting proceeds almost twice as rapidly as in spring. During the second nesting the pause before the first egg laying disappears and the eggs are some-

times laid in still incompleated nests. The overlapping of successive reproductive cycle phases can be followed best of all in cases of triple nesting. The simultaneousness of feeding of the brood fledgelings and of a new nest construction in P.fulvescence saves, on the average, about two weeks. The next reproductive cycle is still more shifted in time: the first egg of the third clutch is laid on the day the second brood fledgelings leaves the nest (Kovshar, 1977).

Polycyclicity is, thus, very characteristic of the reproduction of many avian species under conditions of the subalpine zone. In compensates, to a great extent, the hypsomorphic effect which is expressed only in a certain decrease of the clutch size. The principal differences in the main ways of adaptation of birds to the life in high latitudes and in the southern alpine zone comprise, in my view, the combination of the two features: a reduced clutch size and polycyclicity of reproduction. If subarctic birds are characterized by an increased, as compared with bird populations of moderate latitudes, clutch size combined with a distinctly monocyclic way of reproduction, in the southern alpine zone, where the clutch size is mainly limited by the shortened summer day, another way proved to be more promising: double or triple nesting with a lesser number of eggs in the clutch.

This example allows us to consider polycyclicity as an important way of intensification of bird reproduction not only in the mountains, but also under conditions when an increase of the clutch size is impossible or inexpedient due to either reason (e.g. in pigeons and some other birds with the minimal or a very standard clutch size).

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ECOLOGICAL ADAPTATIONS OF THE SNOW GOOSE (ANSER CAERULESCENS)
TO HIGH-LATITUDE ENVIRONMENT

A.V.Kretchmar, E.V.Syroetchkovsky

Institute of Biological Problems of the North, Far-East Scientific
Centre of the USSR Academy of Sciences, Magadan, USSR;

Institute of Evolutionary Morphology and Ecology of Animals of the
USSR Academy of Sciences, Moscow, USSR

The snow geese breeding colony at Wrangel Island is situated at the northern edge of the species range, in an isolated portion of the arctic tundra remote from the mainland. It is therefore liable in full measure to the influence of the unfavourable conditions prevailing at high latitudes, viz. short frostless seasons, frequent cold snaps at the height of the hatching period, rather low air temperatures in summer, and early autumn frosts. The total length of the snow goose reproductive cycle coinciding almost ideally with that of the frostless season (which is in fact far from being constant), the well-being of the population is primarily dependent on the birds' adaptive faculties and a possibility for them to be revealed.

It should be pointed out here, to begin with, that this report deals largely with ecological adaptations to climatic factors of high latitudes, the influence of predators, the arctic fox in particular, being a minor topic.

The surveys were carried out at the island annually from 1969 through 1981.

The first appearance of the geese on the nesting territory and especially the time of their mass arrival are determined to a great extent by the air temperature and depth of the snow cover. The mass arrival period may be as long as 3-4 or even more than 7-8 days, although it is not so easy a matter to determine the end of the passage. Birds can arrive in last summer broods or small flocks of no more than 30-40 individuals. The spring being rapid and steady, the flocks remain intact for 3-4 days after arrival. They are maintained for as long as 7-8 days in protracted spring, but break up immediately after arrival if it is delayed.

Breeding success of the population is predetermined by weather conditions in the third ten-day period of May and in the first one in June, on which pre-nesting and the beginning of nesting periods fall respectively. The state of the snow cover by the time of birds' arrival is of paramount importance as well as the rates of snow thawing and tundra drying up late in May and early in June. In protracted spring only small spots within the territory of the colony are snowless and sufficiently dry in the first few days of June (or in its first ten-day period for that matter), which results in the lack of nesting sites for many pairs. In such cases the area of the colony is drastically reduced (it can fluctuate from 200 to 2600 hectares), and many birds are not involved in the reproductive activities on a par with the holders of nesting sites. Depending on the conditions of the season 14 to 99% of adult birds are capable of having nests.

In protracted spring all the adult birds having no nesting sites of their own leave the colony in the end and move to the moulting grounds. Their further stay in the colony until the rest of its territory is free from snow and dries up, would be to no purpose because it takes goslings no less than 48 days with positive average daily temperature to mature from hatching till the

start flying. It is apparently for the reason that new nests cease to appear in the colony after 10th June, even if additional territories are likely to be free from snow by this time.

Geese without nests of their own have to contribute to the population recruitment by laying their eggs either into other birds' nests or directly on the ground. Some of the latter eggs are ultimately found in the nests since hatching females are apt at rolling them into their own nests if they are within a range of two metres. It brings about an increase of the clutch-size in the years with unfavourable weather conditions when only a part of the population is involved in active nesting. In this case there is an inverse relationship between the number of nesting geese and the average clutch-size. Under favourable conditions the latter is equal to the number of eggs laid by a female, which averages 3,7 as compared to 5,9 for protracted springs when laying eggs into other birds' nests becomes an every-day occurrence.

The data obtained show that younger females three to five years old resort most often to this way of laying eggs for lack of nesting sites.

The unfavourable seasons resulting in mass egg-laying in other birds' nests were observed to occur even more often than favourable ones. Over the last 14 years (including 1982 for which data have already been made available) there were only six seasons indisputably appropriate for the reproduction of snow geese. All other seasons witnessed mass egg-laying into other birds' nests.

A prominent feature of breeding geese's behaviour being active defence of their individual territories, laying eggs by "homeless" females is hampered. A large number of eggs in the nest would otherwise impair their warming by the female. Successful hatching of clutches containing over 9 or 10 eggs is a rare occasion in snow geese. Whenever the clutch-size exceeds 12-13 eggs, including those laid by stray females, the owner of the nest abandons it.

Egg-laying into other birds' nests can by no means be considered as making up satisfactorily for the injury to the population occasioned by the lack of nesting sites. It is likely to extenuate the negative effect of a protracted spring but only partially. Nevertheless this adaptation enables more birds to participate in the reproductive process and increases the genetic diversity of the next generations. There is one more aspect to this phenomenon. According to our observations, eggs within a clutch differ in that those laid first are of greater weight and give life to the most viable goslings. The eggs laid next are smaller, while the last ones are the smallest, the survival of birds hatched from them being the lowest. Geese that have no nests of their own lay as a rule less eggs than nesting ones. There are usually 1-2 eggs in their clutches (1.5 on average). Yet, they are very big and the goslings are viable. Thus, in the seasons when egg-laying into other birds' nests is at its peak they mostly contain the first-laid, in fact the fittest eggs, which is supposed to increase the survival rate of the flappers in the post-breeding period.

One more consequence of the regular lack of nesting sites for northern snow goose populations should be noted. It is usually considered to affect them negatively. However the lack of nests for a large number of birds seems to have some advantages as well. The fact is that, unlike individuals, that do not nest nesting pairs are exposed to more than one danger both during and

after the breeding season. They fall a prey to predators when defending either their clutches or broods. They can also perish from cold and sometimes of exhaustion. Our observations of the behavior of goslings able to fly suggest that geese accompanying broods are more often shot by hunters after having left the Island. All these factors are far less perilous for the geese that do not nest, and they spend the season in much more suitable conditions. Their mortality rate is believed to be lower than in nesting birds. This difference can be considerable as appears from the fact that many birds do not have nests in the seasons with inappropriate weather conditions when the impact of unfavourable climatic factors is particularly heavy.

According to the results of ten years studies, conducted over about 42% of adult snow geese have no nests on Wrangel Island annually. This is likely to result in greater life-expectancy in northern populations of the snow goose as compared to southern ones which gives the former a chance to have additional nesting seasons. Combined with egg-laying into other birds' nests, this factor is apt to make up for more frequent nesting failures in the North.

It is quite possible that this feature of snow goose biology entails a slower change of generations in northern populations as compared to southern ones.

As regards the indirect influence of unfavourable climatic factors, it is important to stress that isolated or scattered nests are more vulnerable to injury by polar foxes. This injury is relatively small in seasons with suitable weather conditions, but it is likely to increase dramatically in cold protracted springs. Combined with other deleterious influences, this impact can reduce to nought the productivity of the colony in such years.

There are also other aspects of the polar fox impact on snow goose populations that are not directly connected with weather conditions. The Wrangel polar fox population numbers and status depend on the abundance of lemmings. The lemming numbers being high, the majority of polar foxes are involved in the reproductive process and do not therefore move far away from their burrows. They vigorously drive stray animals taking no part in the reproduction process away from their territories. Burrows of the polar fox in the area occupied by the colony are not numerous and total 12 or 14, i.e. the colony is exploited by a relatively small number of predators in the years when their reproductive capacity is high. If, however, lemming numbers are low, a large number of polar foxes do not breed and roam about the island. On finding themselves within the colony they are disposed to settle. In the end their total number on the territory of the colony can exceed 3 to 4 times that observed there in the seasons of their mass reproduction. Such years witness the gravest injury to the colony.

Even superficial observations of the relationship between geese and polar foxes reveal the adaptive nature of colonial nesting to sustain the pressure of predation. Surroundings of the island place the whole of its territory within the reach of polar foxes. Under these conditions the only escape for the geese is nesting in large densely populated colonies, as attacking one nest the predator unavoidably disturbs neighbouring pairs and finds itself attacked by several birds at a time.

We have not happened to observe isolated nests of snow geese, but they are often arranged in small settlements in the close proximity to the nesting sites of snowy owls, which are known to vigorously defend their territories from intruding predators. (Nests of eiders and brent geese are often found in these settlements too.)

As the whole territory of the island is easily accessible to polar foxes, we suggested at the very outset of our surveys that the only way for new snow goose colonies to come into existence seems to be progressive expansion of small settlements surrounding snow owl nests whenever the lemming numbers are high. This has been proved to be exactly the case with a new colony in the Mamontovaya river valley, where nesting conditions are particularly favourable for the snowy owl. The colony supported nearly 1000 nests in 1981.

It can thus be inferred that the most conspicuous adaptation to a high-latitude environment in the snow goose is speedy synchronous nesting within a very short time. There is virtually no pre-nesting period. Birds that fail to nest either do not breed at all or contribute to the reproduction of the population by laying eggs into other birds' nests. Populations whose annual recruitment is not secure are likely to exist provided the mortality rate in non-breeders is low, i.e. when life-expectancy in northern populations is higher than in the southern ones.

Hatching success under extremely severe climatic conditions is promoted by some patterns of female behaviour during the periods of egg-laying and incubation. In particular, the egg-warming regime prevents the clutch from supercooling before incubation proper begins and helps maintain an exceptionally stable temperature in the nest during hatching.

Colonial breeding of snow geese along with the disposition of the colonies in the vicinity of snowy owl nests is worth mentioning among the principal adaptations to the pressure of predation by the polar fox as being of considerable importance in the peculiar surroundings of Wrangel Island.

CONTENTS

| | |
|---|----|
| International Ornithological Congresses 1884-1982 | 3 |
| Acta of Preceding International Ornithological Congresses | 4 |
| Preface | 5 |
| XVIII Congressus Internationalis Ornithologicus | 6 |
| International Co-Operation and Integration with other Sciences - the Main Trend of Ornithology Development (Ilyichev V.D.) | 8 |
| Report of the Activities of the International Ornithological Committee and of its Permanent Executive Committee | 15 |
| Members of the Permanent Executive Committee 1982-1986 and Members of the International Ornithological Committee 1982-1986 | 23 |
| Report of the Standing Committee on Ornithological Nomenclature | 29 |

PLENARY LECTURES

Presidential Address

| | |
|---|-----|
| Haartman L.v. The Biological Significance of the Nuptial Plumage of the Male Pied Flycatcher | 34 |
| Kumari E. Contribution of Russian and Soviet Ornithologists to Palearctic Zoogeography | 61 |
| Sibley Ch.G., Ahlquist J.E. The Phylogeny and Classification of the Passerine Birds, Based on Comparisons of the Genetic Material, DNA | 83 |
| Busse P. Geographical and Ecological Aspects of Bird Migration as a Methodical Problem | 122 |
| Haftorn S. Recent Research on Titmice in Norway | 137 |
| Immelmann K. Sexual Imprinting in Zebra Finches - Mechanisms and Biological Significance | 156 |

Symposium

PALEONTOLOGY AND EVOLUTION OF BIRDS

| | |
|---|-----|
| Brodkorb P. Preliminary Report on Pliocene/Pleistocene Birds of East Africa... | 174 |
| Elżanowski A. The Evolution of Parental Care in Birds with Reference to Fossil Embryos | 178 |
| Feduccia A. The Morphological Evidence for Ratite Monophyly: Fact or Fiction.. | 184 |
| Kurochkin E.N. Lower Cretaceous Birds from Mongolia and their Evolutionary Significance | 191 |
| Rich P.V., Tets van G.F., Balouet C. The Birds of Western Australasia | 200 |
| Vorobyeva E.I. The Problem of Morphological Levels in Organization of Vertebrates | 227 |
| Mourer-Chauviré C. New Discoveries of Eocene and Oligocene Birds in the "Phosphorites du Quercy", France: the <u>Idiornithinae</u> (<u>Ralliformes</u> , <u>Cariamidae</u>) | 234 |

Symposium

SENSORY ORGANS AND COMMUNICATION IN BIRDS

| | |
|---|-----|
| Tembrock G. Biocommunication in Birds | 242 |
| Khayutin S.N. Acoustical and Visual Mechanisms of the Natural Behaviour of Tree-hole Nestlings | 247 |
| Wallschläger D. Acoustical Communication of Woodpeckers | 253 |
| Golubeva T.B. Tikhonov A.V. The Voice and Hearing of Birds in Ontogeny | 259 |
| Temchin A.N. Acoustical Reception in Birds | 275 |

Symposium

NEW PROBLEMS OF ORIENTATION

| | |
|--|-----|
| Wallraff H.G. Theoretical Aspects of Avian Navigation | |
| Able K.P. The Contribution of Radar and Visual Techniques to Orientation Research | 293 |
| Vilks E., Katz Y., Liepa V. The Role of Artificial Light Sources for the Visual Orientation of European Robins (<u>Erithacus rubecula</u>) | 300 |
| Wiltshko W., Wiltshko R. Interaction of Different Orientation Cues | 304 |
| Semm P., Wiltshko W. The Role of Magnetic Information in Bird Orientation .. | 312 |
| Ilyichev V.D. Studies on Bird Orientation in the USSR | 318 |

Symposium

STRATEGIES OF BIRD CONSERVATION

| | |
|--|-----|
| Lovejoy Th.E. Minimum Size for Bird Species and Avian Habitats | 324 |
| Burnham W., Cade T.J. Reintroduction and Translocation of Birds as Conservation Strategies | 328 |
| Temple S.A. Managing Bird Populations versus Managing their Ecosystems | 336 |
| Imboden C. Priorities for Extinction | 336 |

Symposium

BIOGEOGRAPHY AND DEVELOPMENT OF AVIFAUNAS

| | |
|---|-----|
| Bochen'ski Z. The Development of Western Palaearctic Avifaunas from Fossil Evidence | 338 |
| Vuilleumier F. Fossil Evidence on the Development of South American Avifaunas | 348 |
| Martens J. Speciation and the Development of Himalayan Avifaunas | 358 |
| Blondel J. Historical and Ecological Evidence on the Development of Mediterranean Avifaunas | 373 |

Symposium

ENERGETIC AND TIME BUDGETS OF FREE LIVING BIRDS

| | |
|---|-----|
| Weather's W.W., Nagy K.A., Buttemer W.A. Simultaneous Estimates of Daily Energy Expenditure Using Time-Budget Analysis and Doubly Labeled Water | 388 |
| Westertep K., Drent R. Energetic Costs and Energy-Saving Mechanisms in Parental Care of Free-Living Passerine Birds as Determined by the D ₂ ¹⁸ O Method | 392 |
| Vleck C.M. Time and Energy in Avian Incubation | 399 |
| King J.R. The Energy Requirements of Terrestrial Locomotion in Birds | 404 |
| Potapov R.L., Andreev A.V. Time and Energy Budgets of Wintering <u>Tetraonidae</u> .. | 409 |
| Vorobyeva T.D. Daily Budgets of Time and Energy in Wintering Lesser White-Fronted Geese <u>Anser erythropus</u> | 413 |
| Dolnik V.R., Ilyina T.A. Time and Energy Budgets of the Chaffinch, <u>Fringilla coelebs</u> , during Reproductive Period and Problems of Universal Coefficients for the Converting Time Budget to Energy Budget | 416 |
| Gavrilov V.M., Dolnik V.R. Basal Metabolic Rate, Thermoregulation and Existence Energy in Birds: World Data | 421 |

S y m p o s i u m

PHOTOPERIODIC CONTROL AND ENDOGENOUS TIME PROGRAMS

| | |
|---|-----|
| Chandola A., Singh S., Chakravorty K. Reproductive Periodicity in the Weaver Bird: Role of Photoperiod and of Gonadal Hormones | 468 |
| Wingfield J.C. Environmental Factors Influencing the Termination of Reproduction in Finches | 478 |
| Gavrilov V.M., Dobrynina I.N. The Photoperiodic Control of an Endogenous Timer Regulating Postnuptial Molt in Birds | 488 |
| Gwinner E., Dittami J., Gänshirt G., Hall M., Wozniak J. Exogenous and Endogenous Components in the Control of the Annual Reproductive Cycle of the European Starling | 501 |
| Wada M. Gonadotropin Release and Rhythms of Calling Behaviour by Endogenous Oscillator in Quail | 516 |

S y m p o s i u m

ADAPTATION OF BIRDS TO HIGH LATITUDES AND MOUNTAINS

| | |
|---|-----|
| Parmelee D.F. Polar Adaptations in the South Polar Skua (<u>Catharacta maccormicki</u>) and the Brown Skua (<u>Catharacta lonnbergi</u>) of Anvers Island, Antarctica ... | 520 |
| Johnson St.R. Adaptations of the Long-Tailed Duck (<u>Clangula hyemalis</u>) during the Period of Molt in Arctic Alaska | 530 |
| Meltofte H. Populations and Breeding Schedule of Waders in High Arctic Greenland | 540 |
| Salomonsen F. Altitudinal Adaptation in Body Proportions of Birds | 541 |
| Brown R.G.B. The Influence of Ice on the Ecology of Arctic and Antarctic Seabirds | 559 |
| Kovshar A.F. Polycyclicity and Hypsomorphic Effect in Reproduction of Mountain Birds | 567 |
| Kretchmar A.V., Syroetchkovsky E.V. Ecological Adaptations of the Snow Goose (<u>Anser caerulescens</u>) to High-Latitude Environment | 570 |

Издание осуществлено с оригинала,
подготовленного к печати Всесоюзным орнитологическим обществом АН СССР

ТРУДЫ XVIII МЕЖДУНАРОДНОГО ОРНИТОЛОГИЧЕСКОГО КОНГРЕССА Том I (на англ. яз.)

Утверждено к печати Институтом эволюционной морфологии
и экологии животных им. А.Н. Северцова АН СССР

Н/К

Подписано к печати 09.08.85. Формат 70x100 1/16. Бумага офсетная № 1
Печать офсетная. Усл.печ.л. 46,8. Усл.кр.-отт. 46,8. Уч.-изд.л. 48,7. Тираж 1600 экз.
Тип. зак. 681. Цена 3р. 70к.


Ордена Трудового Красного Знамени издательство "Наука"
117864 ГСП-7, Москва В-485, Профсоюзная ул., д. 90

Ордена Трудового Красного Знамени 1-я типография издательства "Наука"
199034, Ленинград В-34, 9-я линия, 12



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